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SWIMBLADDER STRUCTURE OF DEEP-SEA FISHES IN RELATION TO THEIR SYSTEMATICS AND BIOLOGY

by

N. B. Marshall

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N. B. MARSHALL

British Museum (Natural History)

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SWIMBLADDER STRUCTURE OF DEEP-SEA FISHES IN RELATION TO THEIR SYSTEMATICS AND BIOLOGY

By N. B. Marshall

British Museum (Natural History)

(Plates I-III, Text-figures 1-47)

"When one picks up a fish, one may be said, allegorically, to hold one of the knots in an endless web of netting, of which the countless other knots represent other facts, whether of marine chemistry, physics or geology, or other animals and plants. And just as one cannot make a fish-net until one has tied all the knots in their proper positions, so one cannot hope to comprehend this web until one can see its inter-nodes in their true relationship."

BIGELOW (1930)

INTRODUCTION

IN both structure and function the teleost swimbladder is one of the most plastic of vertebrate organs. While it is primarily a hydrostatic organ, making a fish weightless in water, it may also be modified for respiratory, sensory and sound-producing activities (Jones and Marshall, 1953). Apart from the respiratory aspect, this statement is equally true of many deep-sea fishes. And the exception is understandable, for the use of the swimbladder as a lung is obviously limited to physostomatous teleosts, those with a pneumatic duct joining the sac to the foregut. Virtually all deep-sea fishes have a completely closed (physoclistous)¹ swimbladder.

Cuvier and Valenciennes (1848) appear to have been the first to discover a swimbladder in a deep-sea fish. Concerning the salmonoid genus *Argentina*, Valenciennes wrote as follows: 'La vessie natatoire de l'Argentine a un autre caractère anatomique et physiologique fort intéressant pour nos études; elle ne communique pas avec le canal digestif; je n'ai pu du moins trouver de conduit pneumatique dans les trois individus d'espèces différentes que j'ai disséqués et dont les viscères étaient cependant parfaitement conservés.' (In the following volume (1850) they record the presence of a swimbladder in the hatchet fish, *Argyropelecus hemigymnus*.) Nearly forty years later, Günther (1887) made a similar observation in his 'Challenger' Report: 'In none of the abyssal forms examined by me have I found an open communication between the air bladder and the oesophagus, not even in those which are referred to the Physostomatous division.'

In defining the family Sternoptychidae, in which he included the deep-sea fishes, *Sternoptyx*, *Ichthyococcus*, *Maurolicus*, *Gonostoma* and *Chauliodus*, Günther (1864) stated that the swimbladder was simple when present. But under the family Scopelidae (containing fishes now placed in the order Iniomimi) he remarked that the swimbladder was absent, a statement that is true with the notable exception of the lantern fishes (Myctophidae).

There are other observations on the structure of the swimbladder in Günther's 'Challenger' Report (1887) on deep-sea fishes. Further reference will be made to these later, but we may notice here that the rete mirabile of *Gonostoma denudatum* was described as a 'conical muscular body' attached to the posterior ventral part of the swimbladder. This confusion is hardly surprising, for the gas-secreting complex (retia mirabilia and gas-glands) of deep-sea fishes is highly developed. The large rete of *G. denudatum* contains thousands of closely associated arterial and venous capillaries

¹ See page 50.

running forward in parallel to supply the gas-gland, and superficially these small blood-vessels look very like the fibres in a muscle.

However, a year before the publication of Günther's Report, Coggi (1886) had described certain structures in the swimbladders of *G. denudatum* and *Scopelus benoiti* (= *Hygophum benoiti*). He remarked that the 'red bodies' (retia mirabilia) of these two species were very like those of physoclistous teleosts and that the cells in the epithelial body (gas-gland) of *Gonostoma* were very large. In the other species Coggi figured three retia mirabilia, each supplying a corresponding lobe of the gas-gland. We shall see later that this is a constant feature of the myctophid swimbladder. But his finding of an opening into the 'pneumatic duct' is an error. Presumably he found the opening into the gas-resorbing part of the swimbladder, which in myctophids is an 'oval', and is placed at the front of the sac (see pp. 30-42).

Apart from this early account, the only other detailed work on the structure of the swimbladder of bathypelagic fishes has been that of Rauther (1922) on the lantern fish, *Diaphus rafinesquei* and Nusbaum-Hilarowicz (1920) on the hatchet fishes *Sternoptyx* and *Argyropelecus*, and a species of *Cyclothone*. Ray (1950) was the first to find and figure a fat-invested swimbladder, this being in the lantern fish, *Lampanyctus leucopsarus*. In his report on deep-scattering layers in the Monterey Bay area, Barham (1957) referred to work by Jollie (1954, Ph.D. Thesis) on the anatomy of this organ.

There are numerous records of the presence or absence of the swimbladder in both pelagic and benthic deep-sea fishes in Alcock's (1899) *Investigator* Report. Concerning benthic fishes only, Holt and Calderwood (1895) described the swimbladder of the deep-sea gadoid, *Mora* and those of certain macrourids. Presence or absence observations may also be found in Garman (1891) and in a few other papers which will be referred to in the descriptive part of this report. Lastly, Beebe and Vander Pyl (1944) gave the dimensions of the swimbladder in two lantern fishes, *Myctophum affine* and *Lampanyctus macropterus*, while Kanwisher and Ebeling (1957) measured the volume and gas-content of this organ in a number of bathypelagic fishes.

Considering only the observations made during the latter half of the nineteenth century, there is evidence that the swimbladder is found in numerous deep-sea fishes. But despite this early work, various authorities imposed a pattern on nature without further investigation. They decided that a swimbladder could not function in the deep-sea environment owing to the high hydrostatic pressures, and that it was therefore absent in deep-sea fishes. This organ is certainly absent in pelagic fishes whose living-space is centred below the 1000-m. level, but it is present in many fishes that swim above this depth and in numerous species living below, near the deep-sea floor.

The survey in this report has involved the examination of about ninety species of deep-sea fishes, certain aspects of which have already been published (Marshall, 1950, 1951, 1954, 1955; Jones and Marshall, 1953; Denton and Marshall, 1958). The first part is concerned with the description of the swimbladders of bathypelagic fishes. It will be found that this organ is commonly present in a number of major groups (e.g. the Gonostomatidae, Sternoptychidae, Myctophidae and Melamphaidae). In these and other fishes the gas-producing structures are highly developed.

In teleosts, the structural features of the swimbladder are not often of use in classification, but a gratifying feature of this survey has been the discovery that this organ has a distinctive design in the Stomiatoidea, deep-sea Salmonoidea, Myctophidae and Anoplogastridae. This aspect is considered in the second part of the report and leads to discussion of the evolution of bathypelagic fishes.

Then follow sections concerned with the larval organ, the fine structure of the swimbladder wall, and fat-invested swimbladders. In a number of species the swimbladder contains gas during the larval phase which is passed in the surface-waters, but the organ regresses and is invested with fat after metamorphosis to the adult form.

The remaining sections are devoted to functional-morphological and biological aspects. Now, development of the first aspect obviously depends on adequate knowledge of both form and function. Having undertaken a survey to the point where generalizations on morphology could safely be made, it was a pleasure to turn to the work of Dr P. F. Scholander and his colleagues on functional aspects of the swimbladder in deep-sea fishes. Full reference is made to this work at a later stage. In particular, Scholander's (1958) concept of counter-current exchange in the retia mirabilia and his review of this principle in biology has been very helpful.¹ I am also indebted to Dr Ragnar Fänge's (1953) fine work on structure and functions of the euphysoclist swimbladder. In the section on the swimbladder as a hydrostatic organ, findings on the structure of the retia mirabilia and gas-glands are considered in the light of this physiological work, a task that was made easier by my former collaboration with Dr F. R. Harden Jones (Jones and Marshall, 1953).

In the final biological section, the structural development (and absence) of the swimbladder in bathypelagic fishes is considered in relation to vertical distribution and vertical migrations. This has involved some consideration of the physical and biological environment and leads to the final part, which begins with a survey of the swimbladder in benthic deep-sea fishes. Considering only the fishes taken below a depth of 2000 m., at least half the number of species have capacious swimbladders. In the pelagic environment, as already mentioned, this organ is absent in fishes concentrated below the 1000-m. level. This surprising difference led me to consider, to use a concept more familiar to botanists, the 'life forms' of fishes from the upper and lower reaches of the bathypelagic environment. Again, I was helped by former collaboration, this time with Dr E. J. Denton (Denton and Marshall, 1958). The buoyancy balance-sheet of a fish with a capacious, gas-filled swimbladder is such that it can carry a firm skeleton and well-knit muscles. But these two tissue-systems and others are much reduced in pelagic fishes living below a depth of 1000 m., although this is not surprising in view of the poor food-supply around them. These fishes may well have lost the swimbladder simply because there is not sufficient potential energy in their environment to maintain the 'extra' tissues that can be carried by this hydrostatic organ. In pursuing this, and other ideas, I have tried to follow the thought behind the quotation that heads this report.

MATERIAL AND METHODS

Most of the fishes used in this report have been taken during the Discovery investigations. The positions at which they were caught are listed under the name of each species in the descriptive section (pp. 6-50) and unless otherwise indicated the station numbers refer to the Discovery collections.

In nearly all instances, the swimbladder was found by dissecting the fish under a binocular microscope. After noting the position of the organ, and where possible, tracing the blood supply, the swimbladder was removed and cut open so as to display the retial system and gas-glands. As these are well-developed in deep-sea fishes, their structure was readily appreciated. Where sufficient material was available more than one dissection was made.

In certain species (*Cyclothone braueri*, *C. livida*, *Argyropelecus olfersii*, *A. aculeatus*, *Polyipnus laternatus*, *Opisthoproctus soleatus*, *Vinciguerria attenuata*, *V. nimbaria*, *Myctophum punctatum* and *Diaphus dofleini*) the fine structure was studied by means of serial transverse sections. An account of this work appears in the sections dealing with the swimbladder wall (pp. 60-65), fat-invested swimbladders (p. 65-68) and the swimbladder as a hydrostatic organ (p. 68-81).

¹ To Scholander's list of organs in which this physiological principle is operative (the retia mirabilia of the teleost swimbladder, the gills of fishes, the placenta, the vertebrate kidney and the retial vascular structures of mammals) may be added the choroidal gland of the eyes of bony fishes (see Barnett, 1951).

In the descriptive section, measurements are given of the standard length of the fish dissected, the major and minor axes of the swimbladder (which approaches an ellipsoid in form) and the length of the retia mirabilia. Clearly, the dimensions of the sac in a preserved fish will be smaller than those occurring in the living state. However, in most specimens the swimbladder was well expanded. Where conditions were otherwise, this has been noted.

SURVEY OF STRUCTURE

CLASSIFICATION OF FISHES CONSIDERED IN THIS REPORT¹

Order ISOSPONDYLI

Suborder STOMIATOIDEA (p. 7)

Family GONOSTOMATIDAE: *Vinciguerria attenuata* Cocco (p. 7); *V. nimbaria* Jordan & Williams (p. 9); *Pollichthys maui* (Poll) (p. 9); *Bonapartia pedaliota*, Goode & Bean (p. 11); *Maurolicus muelleri* (Gmelin) (p. 11); *Gonostoma denudatum* Rafinesque (p. 13); *G. elongatum* Günther (p. 13); *G. bathyphilum* Vaillant (p. 13); *Photichthys argenteus* Hutton (p. 13) *Ichthyococcus ovatus* (Cocco) (p. 14); *Cyclothone signata* Garman (p. 15); *C. braueri* Jespersen & Täning (p. 16); *C. livida* Brauer (p. 18); *C. microdon* (Günther) (p. 19); *C. acclinidens* Garman (p. 19).

Family STERNOPTYCHIDAE: *Argyropelecus aculeatus* Cuvier & Valenciennes (p. 19); *A. olfersii* Cuvier (p. 20); *A. sladeni* Regan (p. 21); *A. hemigymnus* Cocco (p. 21); *Sternoptyx diaphana* Hermann (p. 21); *Polyipnus laternatus* Garman (p. 22).

Family ASTRONESTHIDAE: *Astronesthes niger* Richardson (p. 23); *A. lucifer* Gilbert (p. 23); *A. gemmifer* Goode & Bean (p. 23); *A. similis* Parr (p. 25); *Borostomias antarcticus* (Lönnberg) (p. 26); *Diplolychnus mononema* Regan & Trewavas (p. 26).

Family STOMIATIDAE: *Stomias affinis* Günther (p. 26); *S. colubrinus* Garman (p. 27); *S. ferox* Reinhardt (p. 27).

Family MELANOSTOMIATIDAE: *Bathophilus metallicus* Welsh (p. 27); *B. pawneeii* Parr (p. 27); *Eustomias obscurus* Vaillant (p. 27); *Echiostoma tanneri* (Gill) (p. 27).

Family CHAULIODONTIDAE: *Chauliodus sloanei* Schneider and *C. barbatus* Garman (p. 27).

Family IDIACANTHIDAE: *Idiacanthus fasciola* Peters (p. 27).

Family MALACOSTEIDAE: *Malacosteus niger* Ayres and *Photostomias guerni* Collett (p. 27).

Suborder SALMONOIDEA (p. 27)

Family OPISTHOPROCTIDAE: *Opisthoproctus soleatus* Vaillant (p. 27); *O. grimaldii* Zugmayer (p. 28); *Winteria telescopa* Brauer (p. 28); *Macropinna microstoma* Chapman* (p. 28).

Family MICROSTOMIDAE: *Xenophthalmichthys danae* Regan* (p. 28).

Family BATHYLAGIDAE: *Bathylagus benedicti* Goode & Bean* (p. 29); *B. glacialis* Lönnberg* (p. 29); *B. antarcticus* Günther (p. 29); *B. argyrogastrus* Norman (p. 29).

Suborder CLUPEOIDEA (p. 30)

Family ALEPOCEPHALIDAE: *Bathytroctes rostratus* Günther* (p. 30); *Xenodermichthys copei* (Gill) (p. 30); *Searsia koefoedi* Parr (p. 30).

Order INIOMI

Suborder MYCTOPHOIDEA (p. 30)

Family MYCTOPHIDAE: *Myctophum punctatum* Rafinesque (p. 30); *Diaphus rafinesquei* (Cocco) (p. 30); *Electrona tenisoni* (Norman) (p. 32); *E. rissoi* (Cocco) (p. 32); *E. antarctica* (Günther) (p. 32);

¹ Species or groups marked with an asterisk were not examined by the author.

Hygophum benoiti (Cocco) (p. 34); *Benthosema glaciale* (Reinhardt) (p. 34); *B. suborbitale* (Gilbert) (p. 35); *Diogenichthys atlanticus* (Tåning) (p. 36); *Myctophum humboldti* (Risso) (p. 36); *M. affine* (Lütken) (p. 36); *Diaphus dofleini* Zugmayer (p. 37); *D. garmani* Gilbert (p. 37); *D. luetkeni* (Brauer) (p. 37); *D. agassizii* Gilbert (p. 38); *Notolychnus valdiviae* (Brauer) (p. 38); *Lampadena chavesi* (Collett) (p. 38); *Lampanyctus güntneri* Goode & Bean (p. 38); *L. alatus* Goode & Bean (p. 38); *L. pusillus* (Johnson) (p. 40); *Gymnoscopelus nicholsi* (Gilbert) (p. 41); *G. townsendi* (Eigenmann & Eigenmann) (p. 41); *Gonichthys coccoi* (Cocco); *Ctenobranchus nigro-ocellatus* (Günther); *Diaphus coeruleus* Klunzinger and *Gymnoscopelus braueri* (Lönnberg) (p. 42).

Family NEOSCOPELIDAE: *Neoscopelus macrolepidotus* Johnson (p. 42); *Scopelengys tristis* Alcock (p. 43).

Family SCOPELOSAURIDAE (p. 43).

Suborder ALEPISAUROIDEA (p. 43)

Order MIRIPINNATI (p. 43)

Order CETUNCULI

Family CETOMIMIDAE: *Ditropichthys storei* (Goode & Bean) (p. 43); *Cetostoma regani* (Zugmayer) (p. 43).

Family RONDELETIIDAE: *Rondeletia bicolor* Goode & Bean* (p. 44).

Order GIGANTUROIDAE: *Gigantura vorax* Regan (p. 44)

Order LYOMERI

Family EURYPHARYNGIDAE: *Eurypharynx pelecyanoides* Vaillant (p. 44).

Family SACCOPHARYNGIDAE: *Saccopharynx ampullaceus* Harwood* (p. 44).

Order ALLOTRIognathi (p. 44)

Family STYLOPHORIDAE: *Stylophorus chordatus* Shaw (p. 44).

Order BERYCOMORPHI (p. 45)

Suborder ANOPOLOGASTROIDEA

Family STEPHANOBERYCIDAE: *Stephanoberyx monae* Gill (p. 45).

Family MELAMPHAIDAE: *Melamphaes megalops* Lütken (p. 46); *M. unicornis* Gilbert (p. 47); *M. mizolepis* (Günther) (p. 47); *M. cristiceps* Gilbert (p. 47).

Family ANOPOGASTRIDAE: *Anoplogaster longidens* (Gill) (p. 47).

Order PERCOMORPHI (p. 48)

Family CHIASMODONTIDAE: *Chiasmodon niger* Johnson (p. 48). *Pseudoscopelus scriptus* and *Dysalotus alcocki* (p. 49)

Order PEDICULATI (p. 50)

Suborder CERATIOIDEA* (p. 50)

Order ISOSPONDYLI

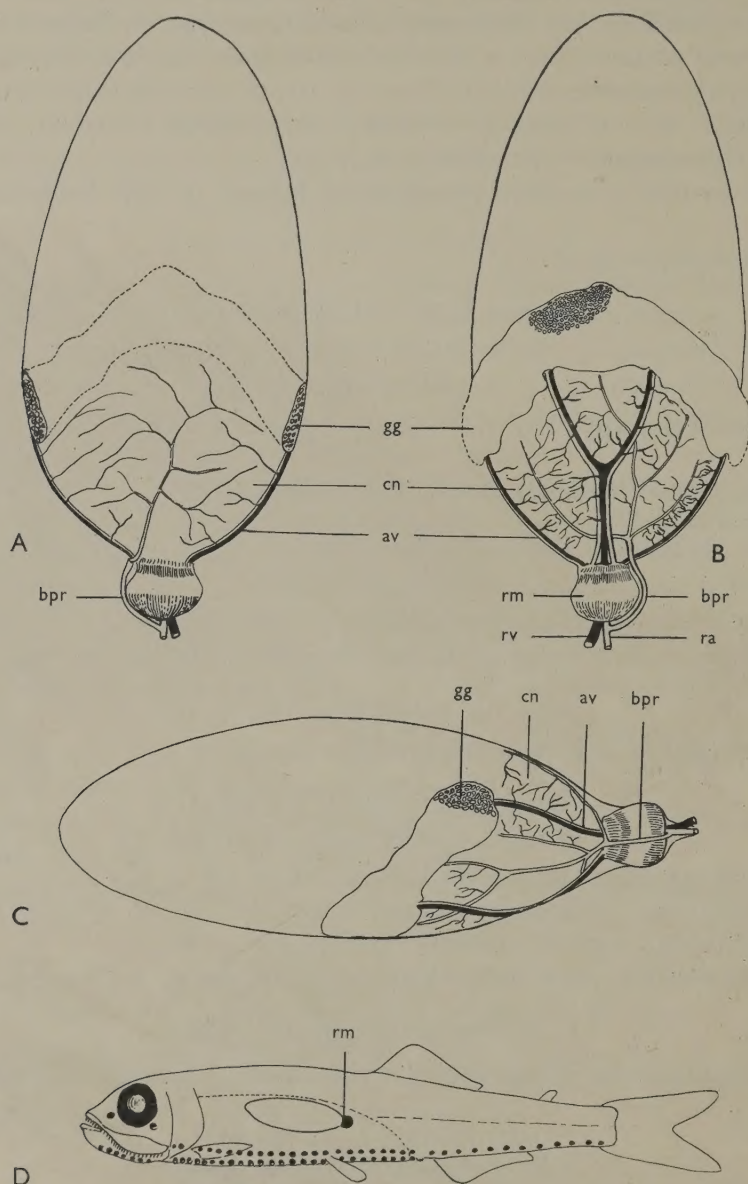
Suborder STOMIATOIDEA Family GONOSTOMATIDAE

Vinciguerria attenuata Cocco (Text-fig. 1)

St. 254, 35° 04' 00" S., 2° 59' 30" E., 21. vi. 27, TYF, 200(-) m. B.M. Reg. no. 1930.1.12. 265-72. Standard lengths of two fishes examined 43.5 and 39.5 mm.

The swimbladder of this gonostomatid lies above the stomach and ends over the origin of the pelvic

fins (Text-fig. 1D). The sac is thin-walled and ellipsoidal in form, the measurements of the major and minor axes in the 43.5-mm. fish being 8.5 and 2.75 mm.



Text-fig. 1. Swimbladder of *Vinciguerria attenuata*, viewed: (A) dorsally; (B) ventrally; (C) laterally, and (D) in position in body-cavity of fish. Veins shown black, arteries white. *av*, artery-vein pair to gas-gland; *bpr*, by-pass branch of retial artery; *cn*, resorbent capillary network; *gg*, gas-gland; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile. (A, B and C, $\times 10$; D, $\times 1.75$.) Note on orientation of swimbladder, in this and subsequent figures. Where the swimbladder is drawn with the major axis vertical, the anterior end is uppermost. If this axis is horizontal, the anterior end is to the left.

In the larger fish, the rete mirabile, which is found at the rear end of the sac, is a massive cylindrical structure with a length and diameter of 0.8 mm. The gas-gland is a fairly broad transverse band of

tissue investing the floor and lateral walls of the sac (Text-fig. 1A-C). The forward, mid-ventral edge of the gland lies about half-way along the length of the swimbladder. The median part runs across the sac, while the lateral sections extend backwards and upwards to end just below the pigmented roof.

The rete mirabile is bipolar¹ in structure. It is formed from an artery and vein which break up into several thousand closely intercalated capillaries, these running parallel courses along the length of the organ. At the forward end they recombine into arteries and veins which supply the gas-gland. Two lateral artery-vein pairs enter the gland behind and just below its two upper edges, while there is a mid-ventral association of a vein with two flanking arteries. The vein runs forward to a point about half-way between the rete and gas-gland and then forks before entering the gland. The two arteries closely follow this venous path (see pp. 78-79 for stomiatoid blood circulation).

Behind the gas-gland there is an extensive capillary network running over the whole of the sac (and just below its inner epithelium). The arterial supply comes from a branch of the retial artery, which forks just before entering the rete. This branch runs forwards along the left side of the rete to a point just in front of it and then gives off a number of sub-branches. In ventral aspect, the vascular pattern may be appreciated by reference to Text-fig. 1B. It will be seen that the artery divides into three main sub-branches. Text-fig. 1C also shows that one main sub-branch travels to the roof of the sac and there subdivides into arterioles and capillaries.

The capillary circulation is completed by the three veins to the gas-gland, which give off lateral venules. Those from the mid-ventral vessel and those from the lower sides of the two lateral vessels are associated with the arterioles of the three ventral sub-branches referred to in the last paragraph. The venules from the upper sides of the two lateral vessels divide to form capillaries that join those of the single dorsal arterial sub-branch.

This capillary circulation forms the resorptive part of the swimbladder, the region where gases diffuse into the blood when deflation of the sac becomes necessary.

The swimbladder of the smaller (39.5 mm.) fish has a very different appearance although its structure is basically the same. But the comparison of these two swimbladders, coming from fishes taken in the same haul, will best be left to a later section (p. 64-65).

Vinciguerria nimbaria Jordan & Williams

St. 1768, 33° 49' 8" S., 12° 50' 8" E., 19. v. 36, N 100 B, 290-150(-0) m. Standard length of fish 34 mm.

The structure of the swimbladder of this species is much like that of *V. attenuata*. The major and minor axes of the ellipsoidal sac measured 5.5 and 2.0 mm.

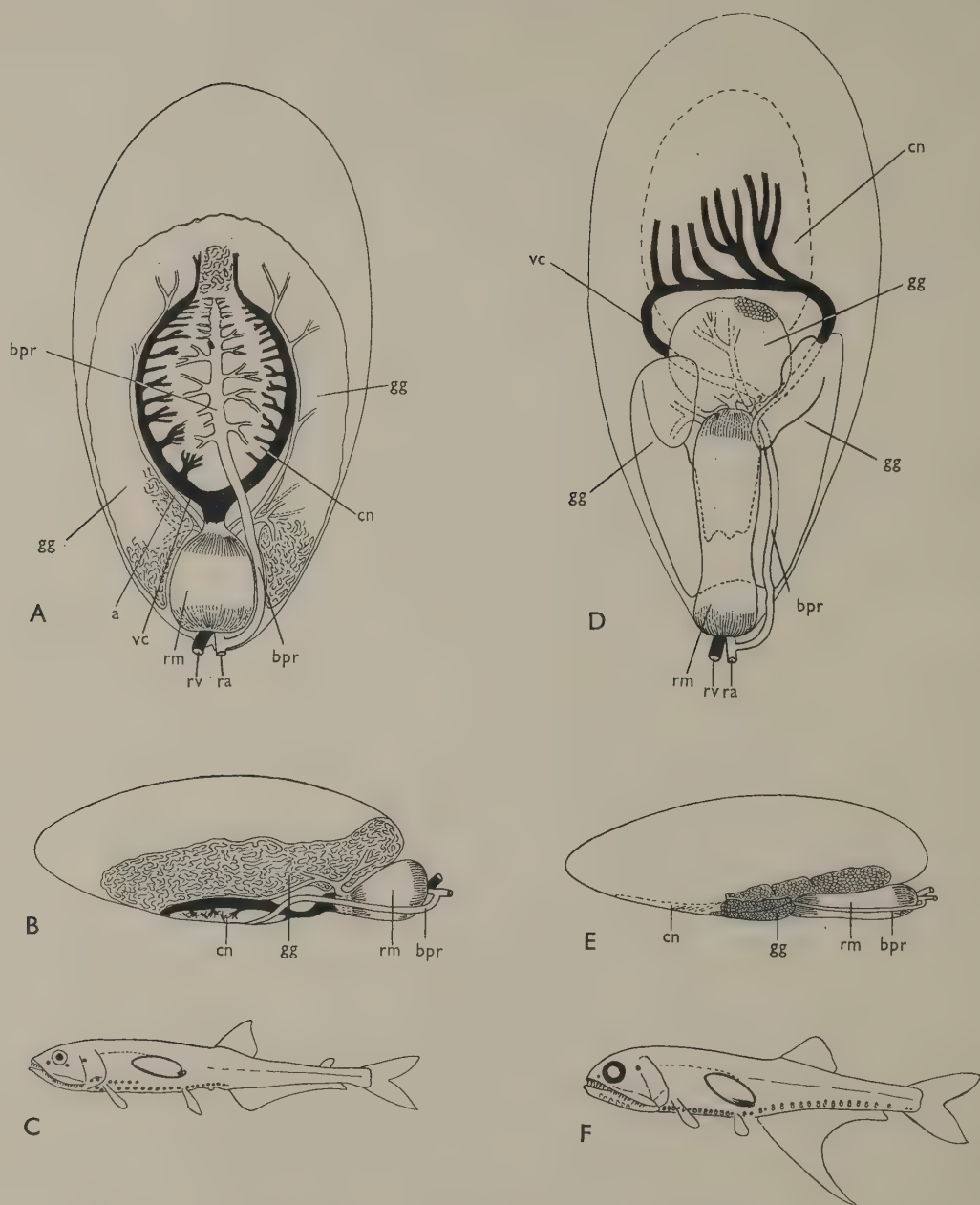
Pollichthys maui (Poll) (Text-fig. 2A-C)

St. 273, 9° 38' 00" S., 12° 42' 30" E., 31. vii. 27, N 100 B, 118(-0) m. B.M. Reg. no. 1930.1.12. 254-9. Standard length 43 mm.

This species has a capacious, thin-walled swimbladder occupying much of the upper part of the body cavity. The sac is ellipsoidal, the measurements of the major and minor axes in the above fish being 5.0 and 2.2 mm. The posterior part of the organ fits snugly into a recess in the fore part of the enlarged, rear section of the kidneys, while the anterior end lies above the stomach.

At the posterior extremity of the sac is a single, bulbous rete mirabile (length 1.2 mm.), which supplies a horseshoe shaped gas-gland investing much of the floor and lateral walls of the swimbladder. The gland fits round the rete and encircles an oval-shaped capillary area, which is set in the middle part of the floor.

¹ See also page 69.



Text-fig. 2. Swimbladders of *Pollichthys mauuli*, viewed (A) ventrally, (B) laterally, and (C) in position in body-cavity of fish, and *Bonapartia pedaliota*, viewed (D) ventrally, (E) laterally, and (F) in position in body-cavity of fish. Veins shown black, arteries white. *a*, artery to gas-gland; *bpr*, by-pass branch of retial artery; *cn*, resorbent capillary network; *gg*, gas-gland; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile, *vc*, vein to capillary network. (A, $\times 20$; B, $\times 12.5$; C, $\times 1.5$; D, $\times 10$; E, $\times 6$; F, $\times 0.9$.)

The rete, like that of *Vinciguerria*, is bipolar. At the forward end is a large median vein which soon forks to send branches round the inner edges of the gas-gland. Each of these two branches is accompanied by an arterial vessel, an association supplying the anterior parts of the gland. The posterior parts on either side of the rete also receive two artery-vein pairs (see Text-fig. 2).

The capillary network, through which gas may leave the swimbladder, is fed with arterial blood through a vessel coming from the retial artery. This by-passes the rete and runs forward along the mid-ventral line to give off arterioles that break up into capillaries. The venous part of the circulation comes from the large median vein of the rete.

***Bonapartia pedaliota* Goode & Bean (Text-fig. 2D-F)**

St. 1582, 05° 39' 1" S., 46° 22' 3" E., 29. iv. 35, N 450 H, 1900-1850(-0) m. Standard length 67.0 mm.

The swimbladder of *Bonapartia* is a thin-walled, capacious ellipsoidal sac lying immediately in front of the enlarged posterior part of the kidneys. When fully expanded it is likely to occupy more of the body cavity than that shown in Text-fig. 2F. The major and minor axes of the sac measured about 10.0 and 5.0 mm.

A large club-shaped rete mirabile (length 3.6 mm.) runs under the posterior part of the swimbladder floor. Again it is bipolar in structure, supplying the gas-gland through vessels that are formed by the capillaries when they reach the anterior end of the organ. The gland, which is a single structure, fits closely round the rete. Its form may best be appreciated by reference to Text-fig. 2D.

Immediately in front of the gland, and on the floor of the sac, is an oval-shaped capillary region. As in *Pollichthys* and *Vinciguerria*, the arterial part of the circulation is provided by a branch of the retial vessel. The venous part could not be traced in its entirety but seems to arise from two vessels running forward through the gland. (These veins may also provide part of the glandular supply.)

***Maurolicus muelleri* (Gmelin) (Text-fig. 3)**

St. 2072, 46° 31' 6" N., 07° 42' 9" W., 22. v. 37, TYFH, 170(-0) m. Standard length 22 mm.

As in other gonostomatids, the swimbladder of *Maurolicus* lies forward of the posterior part of the kidneys. The major and minor axes of the ellipsoidal sac spanned 4.5 and 2.0 mm. The walls were quite thin, having a thickness of between 10 and 20 μ .

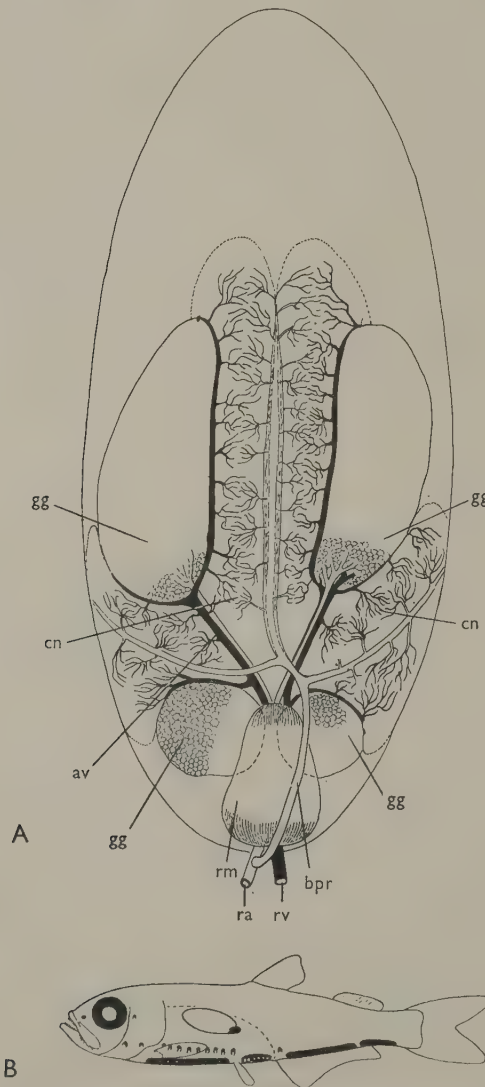
A single rete mirabile (length 0.75 mm.) is found at the posterior end of the sac and is formed by an artery from the dorsal aorta and a vein from the cardinal vessel (between the kidneys).

The gas-gland is four-lobed. Two smaller, rounded lobes lie above and to the side of the front part of the rete. The two larger lobes are oval in shape and extend over the floor and side walls of the middle section of the swimbladder. The long axes of these two lobes are parallel to that of the sac and measure 1.4 and 1.5 mm., the left being the larger. Each lobe receives a closely associated artery-vein pair emerging from the front of the rete, which is thus bipolar in structure.

There is a fine-meshed network of capillaries (the resorbent surface) lying just below the inner epithelium of the sac and between the lobes of the gas-gland. The median ventral area between the two larger lobes extends forward beyond their anterior ends, while the two lateral areas between the small and larger lobes extend upwards over the side walls of the sac. The arterial supply to the capillary network comes from a branch of the retial artery, which runs forward under and beyond the rete to a point close in front of its distal end, where it divides into three sub-branches. Two of these run outwards, each between the corresponding small and large lobe of the gas-gland. The third sub-branch proceeds forward along the mid-ventral line between the two large glandular lobes. These three vessels give off lateral arterioles, which break up into capillaries. The four veins to the gas-gland lobes complete the capillary circulation, each vein sending off branches that partly encircle the

lobe supplied. The forward and lateral edges of the two smaller lobes have a vein running round them, while the whole of the inner edges and about half of the outer edges of the larger lobes are similarly supplied with a venous system. The periglandular veins give off venules that divide again and again to form a dense capillary system, which is eventually linked with that formed by the branch of the retial artery. (The arteries to the lobes play no part in this capillary formation and do not branch until they have entered the gland.) The pattern of arterioles and venules can best be appreciated by reference to Text-fig. 3A.

This extensive capillary complex forms the resorptive region whereby gases diffuse out of the swimbladder and into the blood stream.



Text-fig. 3. Swimbladder of *Maurolicus muelleri*: (A) viewed ventrally, and (B) shown in position in the fish. Veins shown black, arteries white. Note the two small and two large lobes of the gas-gland. *av*, artery-vein pair to gas-gland; *bpr*, bypass branch of retial artery; *cn*, resorbent capillary network; *gg*, gas-gland; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile, (Swimbladder, $\times 30$; fish, $\times 2$.)

Before continuing this survey, certain generalizations may be introduced at this stage. By doing so the descriptions can be more readily followed and needless repetition avoided.

We have seen that the swimbladders of the foregoing species of gonostomatid fishes have certain common features. These are: (1) a single, bipolar rete mirabile, which is formed at the posterior end of the sac, and (2) a resorbent capillary system that obtains its arterial supply through a by-pass branch of the retial artery. These characters are also shared by other stomiatoid fishes with a well-formed swimbladder in the adult phase. Furthermore, the first feature, at least, can be traced in adults with a regressed swimbladder. In the following descriptions, unless otherwise stated, the lengths of the major and minor axes of the sac are given in parenthesis after the standard length of the fish.

***Gonostoma denudatum* Rafinesque (Text-fig. 4A)**

B.M. Reg. no. 85.6.22. 73-6. Messina. Standard length 81 mm. (16.0 × 2.0 mm.)

The swimbladder is elongated and fits close beneath the kidneys, extending down some two-thirds of the length of the body cavity. It originates above the bases of the pectoral fins and ends over the pelvics. Reference to Text-fig. 4A will show the close reciprocal relations between the shapes of the swimbladder and kidneys.

The bipolar rete mirabile, which is club-shaped and about 2.5 mm. in length, runs straight into the posterior end of the swimbladder floor. It is formed from two vessels running down through the kidneys from the dorsal aorta and the cardinal vein. The gas-gland invests most of the swimbladder floor and also extends over the lateral walls of the wider, posterior part of the sac.

Just before its point of entry, the retial artery gives off the by-pass branch to the capillary system. Although not traced, this system must be formed immediately in front of the more extensive, posterior part of the gas-gland.

***Gonostoma elongatum* Günther (Text-fig. 4B, C)**

St. 285, 2° 43' 30" S., 00° 56' 30" W., 16. viii. 27, 125-175(-0) m. B.M. Reg. no. 1930.1.12. 74-7. Standard length 149 mm.

At first sight the swimbladder appears to be completely absent in this species. In place of the long gas-filled sac found in *G. denudatum* is a long rod-like mass formed of golden-yellow fat globules suspended in a reticulum of connective tissue cells. At the posterior end of this rod the fatty tissue extends over a small cream-coloured body that receives an artery and vein running down through the posterior enlarged part of the kidneys (see Text-fig. 4C). These vessels are clearly homologous with those forming the rete mirabile in *G. denudatum*. In fact, the creamy-coloured tissues to which they lead are the remnants of the gas-gland and rete mirabile.

***Gonostoma bathyphilum* Vaillant**

No trace of a swimbladder could be found in this species, not even in a fairly young fish (standard length 77.5 mm.) from St. 3094, 44° 20' N., 16° 49' W., 21. v. 54, TYFH, 1500(-0) m.

***Photichthys argenteus* Hutton (Text-fig. 5)**

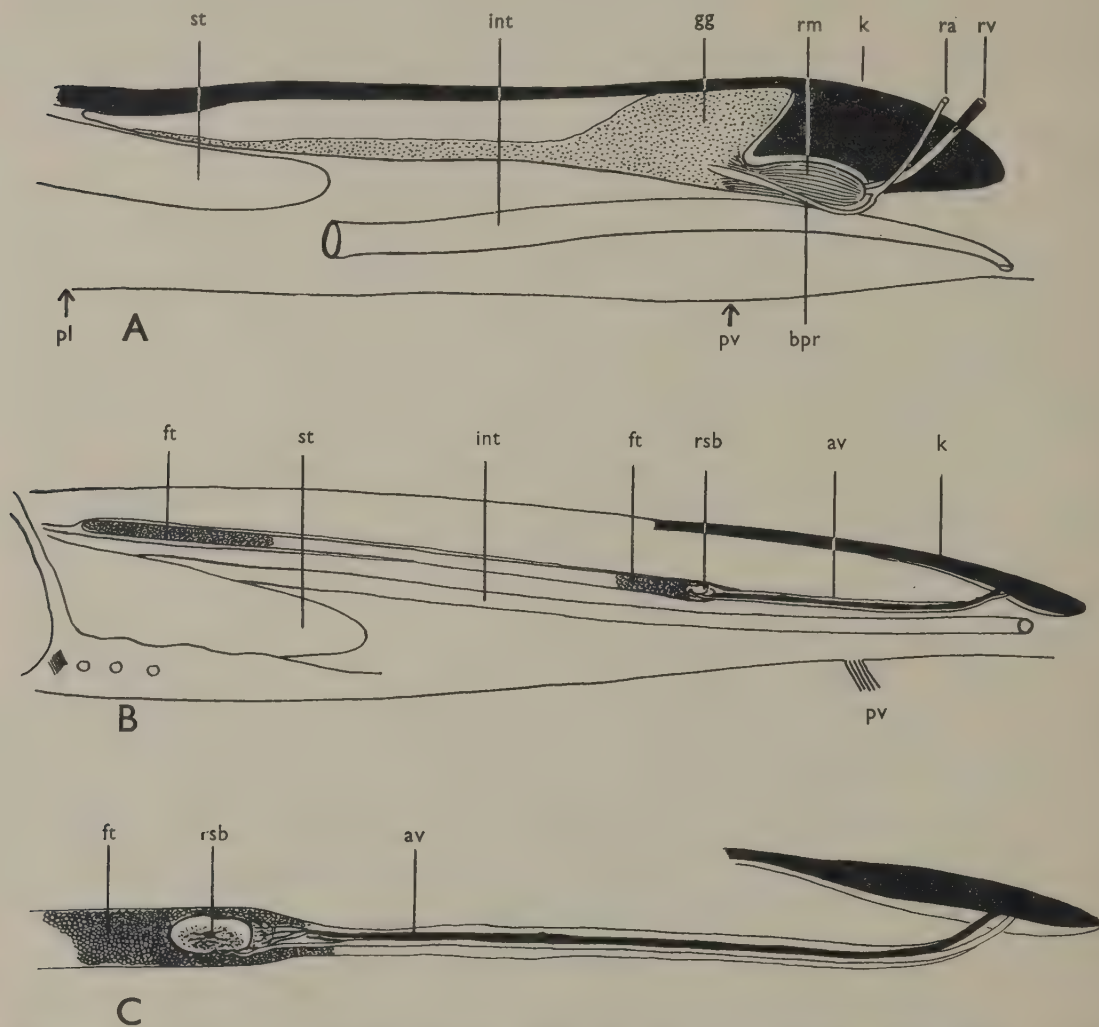
St. 101, 33° 50' to 34° 13' S., 16° 04' to 15° 49' E., 15. x. 26, N 450 H, 350-400(-0) m. Standard length 141 mm. (4.5 × 2.0 mm.).

The swimbladder of *Photichthys* is unusual in form. The sac is a long tube originating over the stomach and extending down about three-quarters of the length of the body-cavity.

At the posterior end is an ellipsoidal bipolar rete mirabile, which is rather more than 3 mm in length and about 1.5 mm. in middle depth. The capillaries of the rete are formed by two vessels coming from the dorsal aorta and cardinal vein (between the kidneys).

The gas-gland invests the walls of the sac over a length of about 10 mm. in front of the rete. As the swimbladder was quite relaxed the walls appear to be rather thick.

Günther (1887) dissected a *Photichthys* taken by the 'Challenger' Expedition and described the swimbladder as a 'long simple sac with thick walls'. As already mentioned in the introduction, the 'conical muscular mass' at the posterior end is clearly the rete mirabile.



Text-fig. 4. Swimbladder of (A) *Gonostoma denudatum* (lateral view), and (B, c) *G. elongatum* (lateral views). In (c) the regressed swimbladder is shown enlarged with part of its investment of fatty tissue. av, artery-vein pair to regressed swimbladder; bpr, by-pass branch of retial artery; ft, fatty tissue; gg, gas-gland; int, intestine; k, kidney; pl and pv, positions of pectoral and pelvic fins; ra, retial artery; rv, retial vein; rm, rete mirabile; rsb, regressed swimbladder; st, stomach. (A, $\times 7.5$; B, $\times 5.4$; C, $\times 15$.)

Ichthyococcus ovatus (Cocco) (Text-fig. 6)

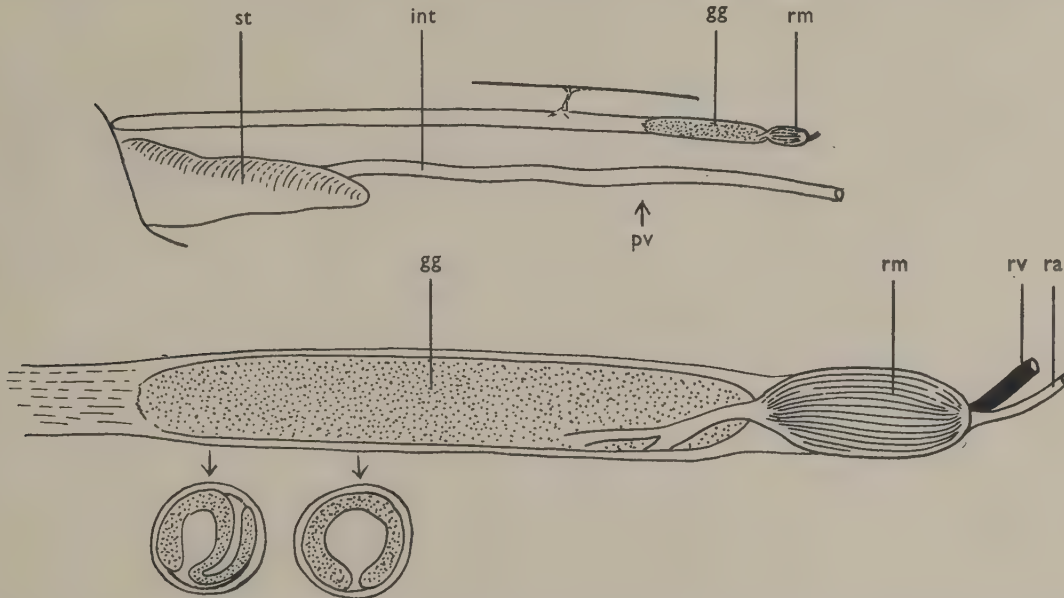
St. 1590, $24^{\circ} 10.4' N$, $17^{\circ} 18' W$, 13. x. 35, TYFB, 400-320 m. Standard length 34 mm. (7.0×2.5 mm.).

While much of the structure could be seen, the swimbladder of this fish was much distorted.

A single rete (length 2.0 mm.) enters the posterior end of the sac to supply a gas-gland (with one median lobe and two lateral lobes) lying on the floor of the sac. Immediately in front of the gland

is part of the resorbent system, which receives two arteries from the by-pass branch of the retial artery. The curious lateral projection of the swimbladder shown in Text-fig. 6 is undoubtedly due to distortion. This is probably the roof of the posterior part of the sac, the part that fits closely within the recess formed by the kidneys.

This projection contained the other part of the resorbent capillary system, for it is supplied from a third branch of the by-pass artery and receives branches from periglandular veins. However, the full appreciation of the circulatory system must be left until a better preserved specimen is available.



Text-fig. 5. Swimbladder of *Photichthys argenteus* (lateral views). Above, general view; below, posterior part of swimbladder, also showing the appearance of the gas-gland in transverse sections. *gg*, gas-gland; *int*, intestine; *pv*, origin of pelvic fins; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *st*, stomach. (Top figure, $\times 2.4$; bottom figure, $\times 12$.)

Cyclothone Goode & Bean

In *Cyclothone* the swimbladder regresses after metamorphosis into the adult form and becomes invested with fat, which is deposited between the tunica externa and peritoneum of the larval organ.

As the peritoneum may be regarded as forming the outermost layer of the swimbladder wall (see Fänge, 1953), and as, in *Cyclothone*, it completely surrounds the fat and the regressed tissues, this entire structure will be called a swimbladder in the description that follows.

Cyclothone signata Garman (Text-fig. 7C-E)

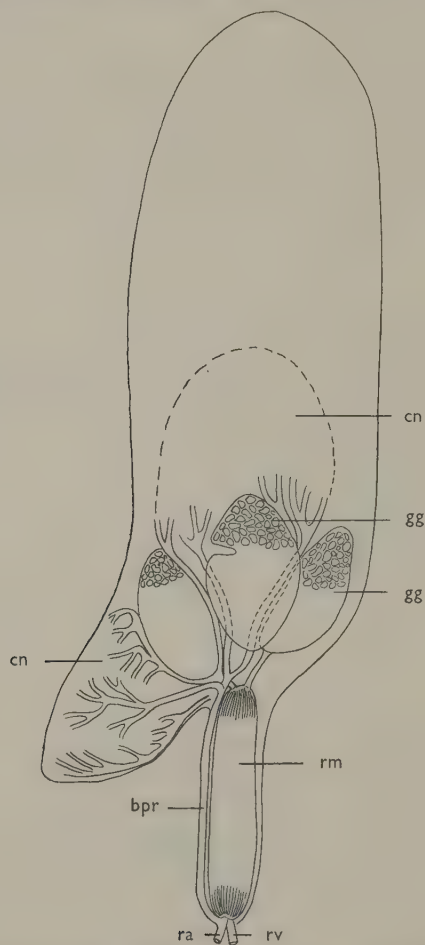
Dana St. 7735, 29. vi. 51, $58^{\circ} 20' N.$, $10^{\circ} 00' W.$, 1500-m. wire. Standard length 31 mm.

The swimbladder of this fish lies just in front of the posterior part of the kidney, the backward end reaching a little beyond the points of insertion of the pelvic fins. In side view the organ is elliptical in shape, having a length of about 3 mm. and a median depth of rather less than 1 mm. Except for the postero-ventral part, it is covered with black peritoneum, which also covers a tubular backward extension running under the bulbous terminal segment¹ of the kidney.

This backward extension contains an artery and vein, which enter the rear part of the swimbladder and then divide into a number of smaller vessels. These are bound together in a long rete mirabile

¹ This is largely formed by the Stannius body (Owen, 1938).

having a length of at least 5 mm. After taking a twisting course through loose connective tissues, the rete enters a heart-shaped gas-gland set in the anterior floor of the bladder. This gas-gland is relatively large, with a length of 1.4 mm. and a width of 1.3 mm. and with the glandular tissue arranged in numerous lacunae. The swimbladder has thick walls consisting mainly of loosely woven connective tissues formed within a viscid matrix. There was no investment of fat and this is unlikely to have disappeared through leaching action, for the fish was preserved in formalin. However, Dr Aughtry, who has studied the ecology of *Cyclothone signata* in the Monterey area, California, has written to me of his finding a fat-charged swimbladder in fishes from 27.0 to 35.0 mm. in standard length.



Text-fig. 6. Swimbladder of *Ichthyococcus ovatus*, viewed from above. The three lobes of the gas-gland are on the floor of the sac. *bpr*, by-pass branch of retial artery; *cn*, resorbent capillary network; *gg*, gas-gland; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile. ($\times 16$.)

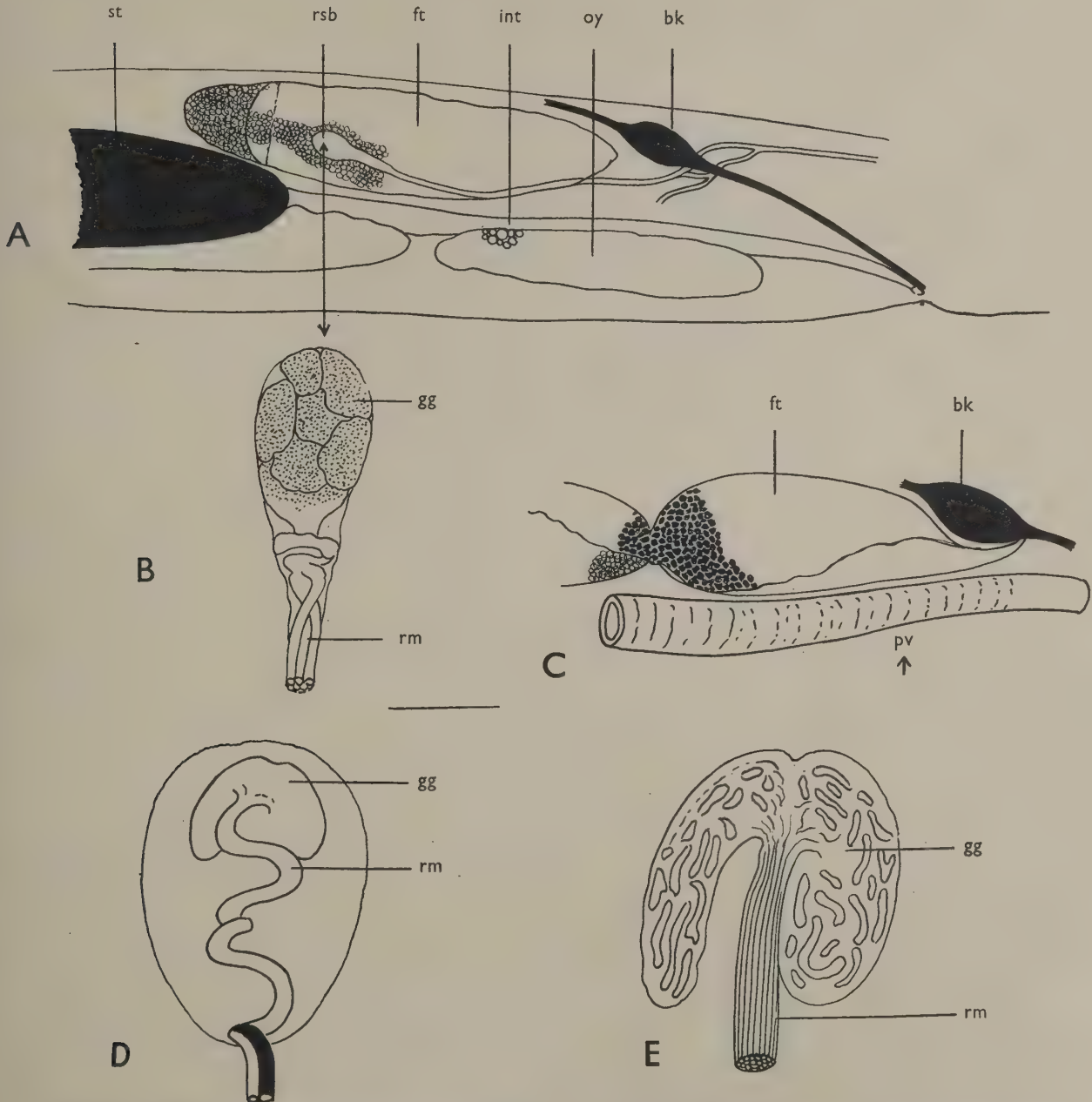
Cyclothone braueri Jespersen & Tåning (Text-fig. 8)

St. 287, $2^{\circ} 49' 30''$ S., $9^{\circ} 25' 30''$ W., 19. viii. 27, TYF, 850(-0) m. Standard lengths of two individuals examined, 33 and 31 mm.

St. 3094, $44^{\circ} 20'$ N., $16^{\circ} 49'$ W., 21. v. 54, TYFH, 1500(-0) m. Standard length 26.5 mm.

The swimbladder lies well back in the body cavity, the posterior end being above the base of the pelvic fins and immediately in front of the bulbous part of the kidneys. In the 31-mm. fish the organ

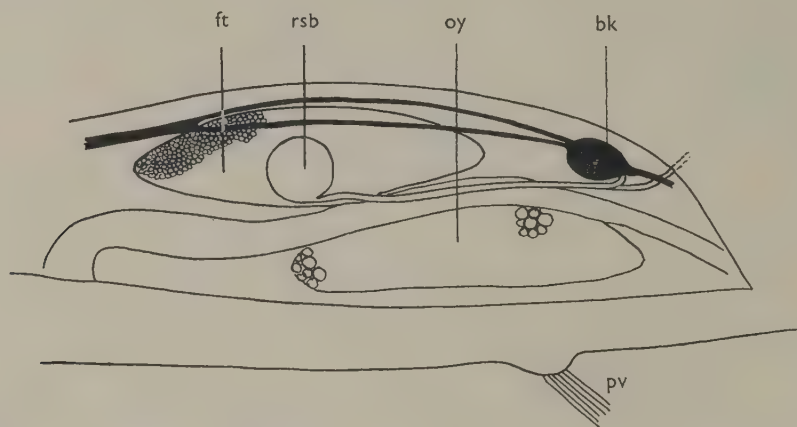
is 3 mm. in length and is invested with reticular connective tissue charged with fat droplets. Two blood-vessels, which are closely bound together, enter the posterior under-surface and run forward to a spherical whitish body set in the middle of the fatty tissue. This body has a diameter of 0.6 mm. and within it are the regressed gas-gland and capillaries of the rete mirabile, these being enveloped by a fibrous coat and bound together with more diffuse connective tissues.



Text-fig. 7. Fat-invested swimbladders of *Cyclothone microdon* (A and B) and *C. signata* (C, D and E). (A and C, lateral views; D and E, ventral views.) *bk*, bulbous, posterior part of kidney; *gg*, gas-gland; *ft*, fatty investment of regressed swimbladder; *int*, intestine; *oy*, ovary; *pv*, origin of pelvic fins; *rm*, rete mirabile; *rsb*, regressed swimbladder; *st*, stomach. (A, $\times 13.5$; B, $\times 37.5$; C, $\times 18.9$; D, $\times 18.9$; E, $\times 30$.)

In the 33-mm. fish the lumen of the sac was not entirely obliterated and the investment of fat was relatively less voluminous, there being a padding of this tissue at the front and rear parts of the sac. On the floor of the sac was a regressed gas-gland. The artery to this structure was traced backwards to the dorsal aorta, while the vein runs to the bulbous part of the kidney, where it may join the renal venous system.

The 26.5-mm. fish has no fatty investment (and it is preserved in formalin) the thick-walled sac measuring about 3 mm. in length. There is a heart-shaped gas-gland on the floor of the anterior half and this receives a long rete mirabile (about 3.5 mm. in length) which enters the posterior end of the organ. The microscopic structure of this swimbladder will be described in a later section (p. 66).



Text-fig. 8. Fat-invested swimbladder of *Cyclothone braueri*. *bk*, bulbous, posterior part of kidney; *ft*, fatty investment of regressed swimbladder; *oy*, ovary; *pv*, pelvic fin; *rsb*, regressed swimbladder. ($\times 18.9$.)

As the larvae of *Cyclothone braueri* have a gas-filled swimbladder, it is clear, as previously mentioned, that the organ gradually regresses and receives a thick coating of fat during the adult phase.

Nusbaum-Hilarowicz (1920) studied the histology of the swimbladder of a species of *Cyclothone*, under the name *C. signata*, but in view of Jespersen's and Tåning's (1926) critical work, the species is most likely to be *C. braueri*. The figures and description show that the swimbladder of this fish was in much the same developmental phase as the 26.5 mm. individual described above.

Cyclothone livida Brauer

St. 3094, 44° 20' N., 16° 49' W., 21. v. 54, TYFH, 1500(-0) m. Standard length of two fishes examined 55 and 37 mm.

In both these individuals the swimbladder has much the same position in the body-cavity as that of *C. braueri*. It is sausage-shaped, having a length of about 5 mm. in the larger fish and about 4 mm. in the smaller one. The middle diameter in both is about 1.5 mm.

Under the layer of black peritoneum that invests the swimbladder come the silvery or faintly golden globules of the fatty tissue. This entirely fills the swimbladder and, as in *C. braueri*, the fat droplets are held in a rather wide meshed reticular connective tissue. In the middle of the swimbladder is a cream-coloured body receiving blood-vessels entering the posterior end of the organ.

The swimbladder of the larger fish was taken for transverse sectioning and the following extra details of structure seen. At its posterior entry and for most of its course to the regressed gas-gland, the blood system consists of six small vessels bound closely together. Three arterioles each have an

associated venule. Close to the gas-gland there are twelve vessels formed no doubt by the forking of each of the six vessels. The twelve vessels continue into the pear-shaped mass of the gas-gland.

Besides these two fishes, dissection of several other smaller individuals has revealed transition stages between the gas-producing swimbladder of the larvae and the fat-invested structure of the adult (see p. 66).

The microscopic structure of the swimbladder of the 55-mm. fish will be described in a later section (pp. 66-67).

Cyclothone microdon (Günther) (Text-fig. 7A, B)

St. 239, 46° 56' 00" S., 46° 03' 00" W., 2. vi. 27, N 450, 1350-1050(-0) m. Standard length of fish 52 mm.

As in other adult *Cyclothone*, the fat-invested swimbladder of *C. microdon* is slung in the rear part of the body-cavity, the backward end lying just before the enlarged posterior part of the kidneys.

In the middle of the blimp-shaped mass of fatty tissue is a small pear-shaped, cream-coloured body, receiving blood-vessels that enter the posterior under-surface of the organ. A vein, which may be an extension of the renal venous complex, runs forward from the bulbous posterior part of the kidney. The origin of the artery that runs side by side with it could not be traced with certainty. After entering the swimbladder these two vessels continue forward within the fatty tissue and spiral round each other just before entering the pear-shaped structure. This consists of regressed glandular cells and associated capillaries, which are invested and bound together with connective tissues. In the above fish this structure measured 0.75 mm. in length and 0.3 mm. in greatest width, while in another individual of the same size the length was 0.4 mm.

Cyclothone acclinidens Garman

John Murray Expedition, St. 95 Arabian Sea, 2-m. tow-net, 1400-m. wire. B.M. Reg. no. 1939.5.24. 115-250. Standard length of fish 30 mm.

The swimbladder of this species has a very similar structure to that in the four species just described,

Family STERNOPTYCHIDAE

Argyropelecus aculeatus Cuvier & Valenciennes (Text-fig. 9)

St. 257, 35° 01' 00" S., 10° 18' 00" E., 24. vi. 27, N 100 H, 111 m. B.M. Reg. no. 1930.1.12. 367-8. Standard length 23 mm. (3.5 × 2.5 mm.).

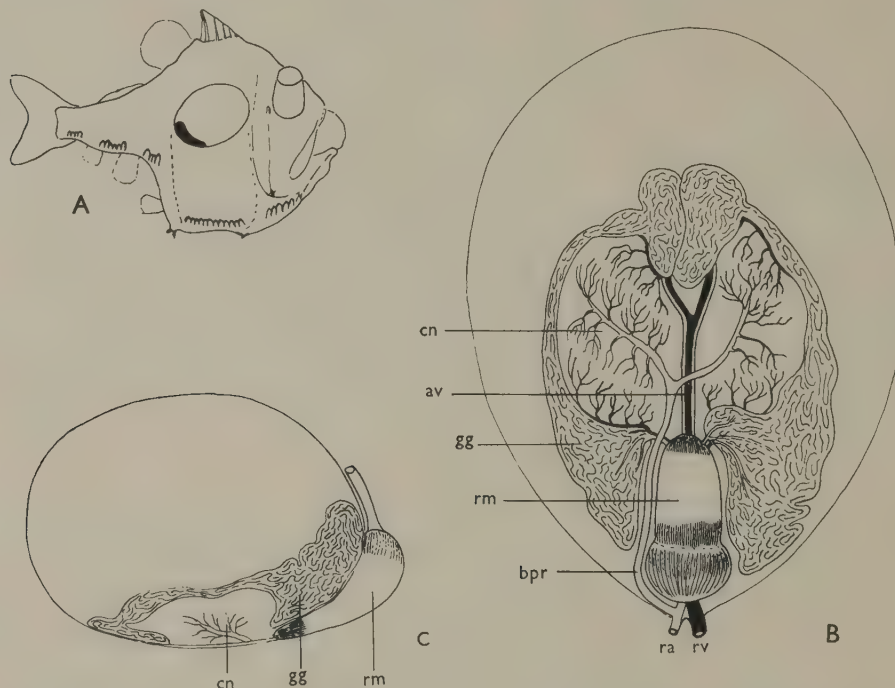
The swimbladder of this hatchet fish is ellipsoidal in form and is slung in the upper part of the body-cavity. At the posterior end of the sac is a massive rete mirabile. It originates at the level of the long axis and extends under the sac over a length of 1.2 mm. Seen from below, the rete is acorn-shaped, the bulbous head consisting of the first division of the artery and vein into finer vessels. These then divide again into the thousands of closely intercalated capillaries that form the rest of this structure.

The gas-gland encircles a heart-shaped capillary bed which extends over the middle region of the swimbladder floor. There are two glandular lobes, each consisting of a band of tissue with expanded posterior and anterior regions (see Text-fig. 9B).

Arteries and veins leave the front of the rete and run into the gas-gland. There are lateral vessels to the posterior expanded parts of the gland and three central vessels running forwards along the mid-ventral line. The middle vessel is a vein which forks to send a branch to each of the anterior expanded parts. On either side of the vein is an artery, each of which follows the bifurcations to the gas-gland.

The arterial supply to the capillary network comes from the artery to the rete mirabile, which sends off a branch just before its point of entry. This branch runs forwards along the right side of

the rete and then forks into two sub-branches (see Text-fig. 9B) serving the left and right halves of the capillary area. Each sub-branch gives off arterioles dividing to form capillaries. The venous part of the capillary circulation comes from the glandular veins from branches running along the inner edges of the two lobes. These branches break up into venules and capillaries that join the arterial complex. The capillary arterial stream is thus by-passed round the rete mirabile, but the return venous flow eventually runs through this structure by way of the glandular veins.



Text-fig. 9. Swimbladder of *Argyropelecus aculeatus*, viewed (A) in position in fish, (B) ventrally, and (C) laterally. Veins shown black, arteries white. *av*, artery-vein association supplying gas-gland; *bpr*, by-pass branch of retial artery; *cn*, resorbent capillary network; *gg*, gas-gland; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile. (A, $\times 1$; B, $\times 22.5$; C, $\times 17$.)

Argyropelecus olfersii (Cuvier)

Taken by M.V. 'Sarsia' off Concarneau. Standard length 38 mm. (4.5×3.0 mm.).

The swimbladder is suspended in the upper half of the body cavity. The sac is oval in outline, and as it is quite relaxed the walls are fairly thick.

A long, club-shaped rete mirabile, with a length of 2.75 mm., enters the posterior end of the sac to supply the gas-gland. An artery from the dorsal aorta and a vein from the cardinal system (between the kidneys) run into the posterior end of the rete.

The gas-gland extends over the roof, side walls and floor of the rear half of the sac, the part over the first two regions appearing to be subdivided into five or six lobes. There is a single lobe on the floor. Each lobe receives an artery and vein from the rete mirabile, while an interglandular capillary network extending over the inner surface of the roof also obtains blood from anterior retial vessels. Longitudinal sections also revealed that there is a capillary network in the floor of the sac (in front of and around the gas-gland). A branch of the retial artery, which subdivides just before entering the rete, runs under the latter and then forwards to break up into capillaries, which run over the inner

surface between the ventral and lateral sections of the gas-gland. The entire capillary circulation, which seems to be much like that of *A. aculeatus*, must form an effective inner surface for the diffusion of gases into the blood.

Argyropelecus sladeni Regan

St. 285, 2° 43' 30" S., 00° 56' 30" W., 16. viii. 27, N 450 H, 175-125(-0) m. B.M. Reg. no. 1930.1.12. 401-6. Standard length 20 mm. (1.75 × 1.5 mm.).

The swimbladder of this species is almost spherical and lies above the stomach in the upper half of the body cavity.

The single rete mirabile receives an artery from the dorsal aorta and a vein that originates between the kidneys. The retial complex formed from these two vessels is cylindrical and enters the floor of the sac from behind to supply the gas-gland. This covers part of the floor and extends backwards and upwards over the side and rear walls of the sac. Viewed from above through a hole cut in the roof of the sac, vessels leaving the rete can be seen running forwards over the floor to the ventral part of the gland.

The two non-glandular areas on either side of these vessels are invested with a capillary network, which has been described more fully under *A. aculeatus*.

Argyropelecus hemigymnus Cocco

Nusbaum-Hilarowicz (1920) found the swimbladder of this hatchet fish to be dilated anteriorly and narrowed posteriorly. Two ligaments of connective tissue attached to the front part of the sac extend upwards to a fastening on the roof of the body-cavity. The walls are constructed of an outer layer of long fibres (mainly running around the sac), a middle and thick layer of loose connective tissue and an inner epithelial layer which forms the gas-gland. This covers the floor and lateral walls of the forward part of the swimbladder, there being a small, median, ventral lobe and two larger lateral lobes. A single long rete mirabile enters the rear part of the swimbladder and runs forwards under the floor to the gas-gland.

Sternoptyx diaphana Hermann (Text-fig. 10C, D)

St. 281, 00° 46' 00" S., 5° 49' 15" E., 12. viii. 27, TYF, 950-850(-0) m. B.M. Reg. no. 1930.1.12. 416-25. Standard length 14 mm. (2.7 × 2.5 mm.).

St. 269, 15° 55' 00" S., 10° 35' 00" E., 26. vii. 27, TYF, 700-600(-0) m. B.M. Reg. no. 1930.1.12. 413-15. Standard length 39 mm. (9.0 × 5.0 mm.).

The swimbladder is a heart-shaped organ lying in the upper half of the body-cavity. The long axis of the sac, which is thin-walled, is directed downwards and slightly backwards, so making an acute angle with the vertical axis of the fish.

There is a pair of suspensory ligaments running from the roof of the body-cavity to an attachment on the posterior part of the roof of the swimbladder. The other suspensory structures, which are more in the nature of mesenteries, are attached to the anterior middle region and the bottom of the sac. Both taper to points of attachment on the peritoneum of the body-cavity, the former to a point opposite the top of the stomach, and the latter to a point behind the basal part of the intestine.

The single, club-shaped rete mirabile, which has a length of 2 mm. in the larger fish, enters the roof of the swimbladder. It receives a branch from the posterior cardinal vein and an artery (running between the kidneys) from the dorsal aorta. The gas-gland invests the roof and is composed of three lobes, each receiving blood-vessels from the rete mirabile.

The fine structure of the swimbladder of this species has been described by Nusbaum-Hilarowicz (1920). Besides noting the bipolar structure of the rete mirabile, he saw that certain of the outgoing

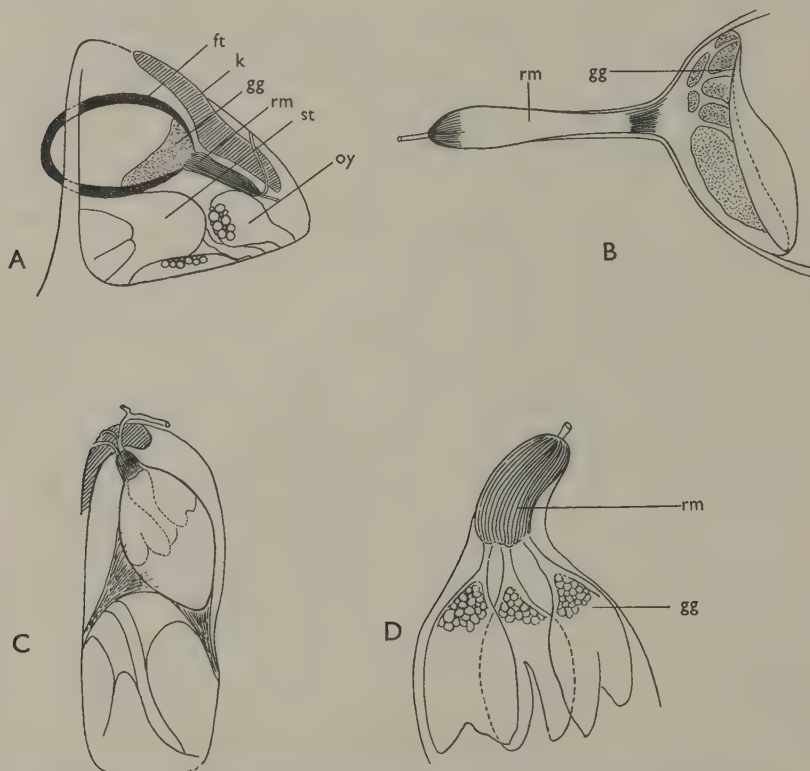
retial vessels formed a capillary network over the inner surface of the sac between the lobes of the gas-gland.

Polyipnus laternatus Garman (Text-fig. 10A, B)

Position, $13^{\circ} 25' N.$, $18^{\circ} 22' W.$, 28. x. 25, N 450 V, 900(-0) m. B.M. Reg. no. 1930.1.12. 458-67. Standard lengths 32.5 and 26.5 mm.

St. 1582, $05^{\circ} 39.1' S.$, $46^{\circ} 22.3' E.$, 29. v. 35, N 450 H, 1900-1850(-0) m. Standard length 36.0 mm.

The swimbladder of this species is suspended in the upper half of the body-cavity, just above the stomach. The sac is more or less oval in side view, with its long axis parallel to that of the fish. In the three individuals examined (in the order given above) the sac had a length and middle depth of 7.0 and 4 mm., 1.75 and 1.0 mm. and 6.0 and 3.5 mm.



Text-fig. 10. Swimbladders of *Polyipnus laternatus* (A and B) and *Sternoptyx diaphana* (C and D). A and C, lateral views, showing position of swimbladder in body-cavity; C and D, rete mirabile and gas-gland. *ft*, fatty investment of swimbladder; *gg*, gas-gland; *k*, kidney; *oy*, ovary; *rm*, rete mirabile; *st*, stomach. (A, $\times 3.5$; B, $\times 11.5$; C, $\times 5$; D, $\times 7.5$.)

A long club-shaped rete mirabile enters the posterior end of the swimbladder, the measurements of its length in the two largest fishes being about 3.5 mm. The gas-gland lies immediately in front of the rete and is partly or entirely divided into two left and right halves.

A layer of fatty tissue invests the swimbladder walls of the 26.5 and 32.5 mm. fishes. The deposition of the fat takes place between the peritoneal layer surrounding the sac and the tunica externa, transverse sections through the swimbladder of the 36 mm. fish revealing that the space between these two layers is filled with loose reticular connective tissue (see also p. 67). The resorbent capillary circulation has not been closely investigated. However, there is an artery running forward by the

side of the rete mirabile, which is undoubtedly homologous with the artery forming part of the capillary network in other stomiatoids. Sections also reveal that there is a capillary network on the floor of the sac between the lobes of the gas-gland and there also appears to be another network in the roof.

Family ASTRONESTHIDAE

Astronesthes niger Richardson (Text-fig. 11)

Dana St. 1378^{III}, 200-m. wire. B.M. Reg. no. 1929.1.4. 93. Standard length 41 mm. (5.5×2.5 mm.).

The swimbladder of this fish, which is elliptical in profile and has thin walls, is slung above the stomach, the extremities lying over the origins of the pectoral and pelvic fins.

A rod-like rete mirabile (1.5 mm. in length) enters the posterior part of the sac. Its blood supply comes from an artery that runs backwards and then upwards between the kidneys to the dorsal aorta and from a vein joining the cardinal vessel at the front end of the enlarged, rear part of the kidneys.

The gas-gland has two lobes, the left being the larger. This is an elongated band of tissue with an enlarged and rounded posterior part, which lies immediately in front of the rete mirabile and invests the lateral walls of the sac. The right lobe is a triangular patch of tissue lying opposite the tip of the left lobe. The length of this lobe is 1.3 mm. as compared with the 3.2 mm. span of the other one.

Each lobe receives blood-vessels leaving the forward end of the rete. The artery and vein to the right lobe run along the lateral walls of the sac.

The resorbent capillary network, which lies just under the inner epithelium, covers most of the swimbladder roof. The by-pass vessel from the retial artery runs forwards along the right side of the rete and then describes an undulating course about the long axis of the sac. This artery gives off arterioles on either side, which break up into capillaries. The circulation is completed by venules and capillaries that come from vessels running along the upper edges of the gas-gland lobes.

Astronesthes lucifer Gilbert (Text-fig. 12A, B)

B.M. Reg. no. 1922.6.7. 14-23. Misaki, Japan. Standard length 73 mm. (16.5×3.5 mm.).

The swimbladder of this astronesthid is an elongated ellipsoid sac tapering to a point anteriorly. Above the base of the pelvic fins and at the posterior end of the organ is a single, bulbous rete mirabile, 2.5 mm. in length and 1.3 mm. in width. This is fed with arterial blood by a vessel that extends backwards and then turns upwards through the kidneys to join the dorsal aorta. The vein enters the kidneys at the point where they begin to enlarge behind the swimbladder.

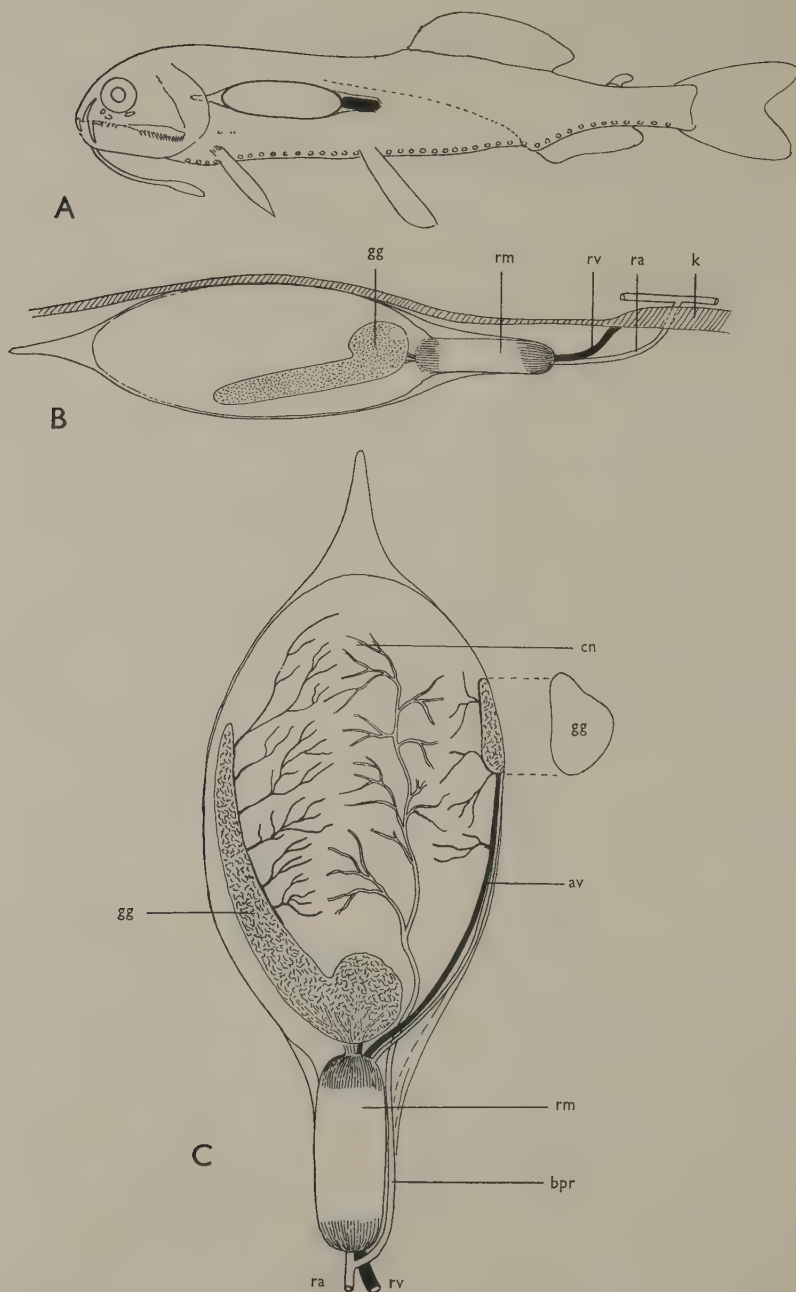
The two lobes of the gas-gland, which extend over the floor and sides of the swimbladder, come immediately in front of the rete mirabile. Along the upper and lower parts of each lobe are vessels, which lead to the rete.

Astronesthes gemmifer Goode & Bean (Text-fig. 12D)

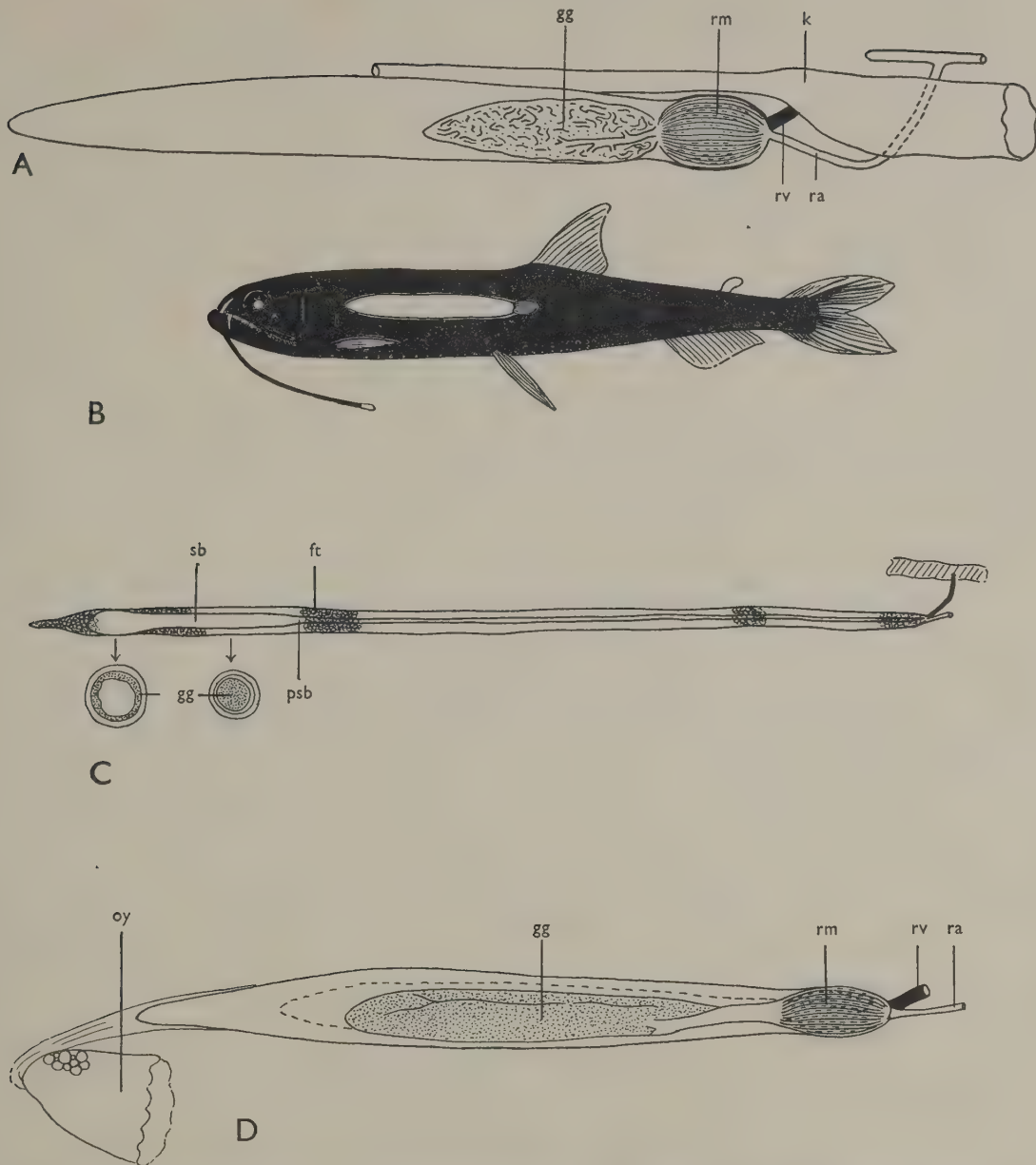
Westmann Isles, Iceland. B.M. Reg. no. 1950.6.30. 2. Standard length 168 mm. (20×3 mm.).

The swimbladder of this species was found over the posterior half of the stomach. It is an elongated organ with very thick walls. At the posterior end of the bladder is a conical rete mirabile measuring about 3.5 mm. in length and 1.5 mm. in greatest width.

The gas-gland appears to be a solid rod-like structure, but actually consists of two closely contiguous lobes which together fill most of the lumen of the sac. All the tissues appear to be very contracted, or it may be that the organ regresses during adult life.



Text-fig. 11. Swimbladder of *Astronesthes niger*, seen (A) in fish; (B) laterally, and (C) ventrally. Veins shown black, arteries white. *av*, artery-vein pair to gas-gland; *bpr*, by-pass branch of retial artery; *gg*, gas-gland; *k*, kidney; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile. (A, $\times 2$; B, $\times 8$; C, $\times 12.5$.)



Text-fig. 12. Swimbladders of *Astronesthes lucifer* (A and B); *Borostomias antarcticus* (C) and *Astronesthes gemmifer* (D). Lateral views. In (C) two transverse sections of the swimbladder show the inner disposition of the gas-gland. *ft*, fatty investment of swimbladder; *gg*, gas-gland; *k*, kidney; *oy*, ovary; *psb*, posterior end of swimbladder; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *sb*, swimbladder. (A, $\times 7.5$; B, $\times 1$; C, $\times 2$; D, $\times 4.8$.)

Astronesthes similis Parr

Dana St. 939, 500-m. wire. B.M. Reg. no. 1929.1.4. 81. Standard length 105 mm. (20 $\times$ 5 mm.).

The swimbladder bauplan of this species is similar to that of other *Astronesthes* spp. The pointed forward end of the sac, which is thin-walled, lies opposite the posterior edges of the gill covers. There is a bilobed gas-gland immediately in front of the bulbous rete mirabile, which enters the

posterior floor of the swimbladder. The left lobe of the gland is the larger, measuring about 6 mm. in length against the 4 mm. span of the right lobe.

Borostomias antarcticus (Lönnberg) (Text-fig. 12C)

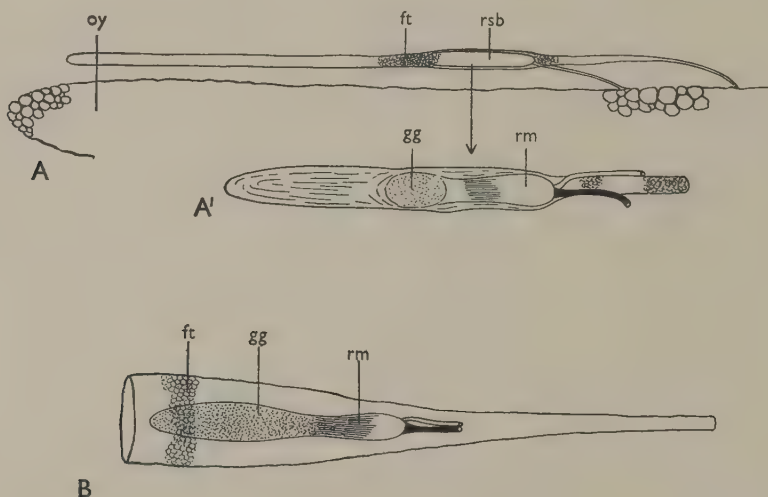
St. 114, 52° 25' 00" S., 9° 50' 00" E., 12. xi. 26, N 450, 650-700 m. B.M. Reg. no. 1930.1.12. 474. Standard length 167 mm.

The swimbladder of this individual proved to be a tubular structure lying above the anterior part of the stomach. It is club-shaped, measures about 13 mm. in length and contains a regressed gas-gland and rete. An artery and vein run into the posterior part of the organ and can be traced back to the backward section of the kidneys. Both the remains of the swimbladder and these blood-vessels are surrounded by a layer of fatty tissue.

Diplolychnus mononema Regan & Trewavas

Standard length 137 mm.

No trace of a swimbladder could be found in this individual.



Text-fig. 13. Fat-invested swimbladders of *Stomias affinis* (A and A') and *S. colubrinus* (B). Lateral views. *ft*, fatty investment of swimbladder; *gg*, gas-gland; *oy*, ovary; *rm*, rete mirabile; *rsb*, regressed swimbladder. (A, $\times 4.5$; A', $\times 11.5$; B, $\times 17.5$.)

Family STOMIATIDAE

Stomias affinis Günther (Text-fig. 13A)

St. 276, 5° 54' 00" S., 11° 19' 00" E., 5. viii. 27, TYF, 150(-0) m. B.M. Reg. no. 1930.1.12. 542-3. Standard length 106 mm.

In this individual there is a regressed swimbladder lying above the ovaries. Fatty tissue invests the organ and is continued forwards and backwards into rod-like prolongations. The anterior one extends to the front of the ovary, while the backward one, which is more slender and tapering, ends rather more than half-way down the body-cavity.

The length of the swimbladder is about 4.5 mm. Entering the posterior end is an artery and vein supplying a club-shaped rete mirabile which is about 1.5 mm. in length. In the middle of the bladder is a small gas-gland, 0.8 mm. in length, which all but obliterates the lumen. Forward of the gland there is no lumen, but merely a 'solid' mass of connective tissue.

***Stomias colubrinus* Garman (Text-fig. 13B)**

Position, 13° 25' 00" N., 18° 22' 00" W., 28. x. 25, N 450 V, 900(-0) m. Standard length 103 mm.

Beginning above the base of the pectoral fins and running just below the kidneys is a well-defined strand of fatty tissue, with a length about four-fifths that of the body-cavity. Within this tissue, about three-fifths of the way along its length, was found the regressed tissues of the swimbladder. Running forward to a posterior rete mirabile is an artery and vein. The rete leads to solid club-shaped structure which consists of a mass of regressed gland cells invested with connective tissues. The rete and gland were about 2.5 mm. in length.

***Stomias ferox* Reinhardt**

Position, 41° 37' N., 12° 30' W., 10. x. 25, N 200 H, 900(-0) m. B.M. Reg. no. 1930.1.12. 541. Standard length of fish 85 mm.

As in *S. affinis* and *S. colubrinus*, there is a well formed strand of fatty tissue, lying just below the kidneys and originating above the base of the pectorals. In the above individual this fat body extended for about 25 mm. down the body-cavity to end in a tapering section attaching to the intestinal mesentery.

No remains of retia mirabilia or gas-gland could be found in this tissue.

Family MELANOSTOMIATIDAE

No swimbladder could be found in adult individuals (judged by the development of the gonads) in each of the following species: *Bathophilus metallicus* Welsh, *B. pawneeii* Parr, *Eustomias obscurus* Vaillant, *Echiostoma tanneri* (Gill).

Beebe and Crane (1939) gave an account of the internal organs of a number of species but made no mention of a swimbladder.

Family CHAULIODONTIDAE***Chauliodus sloanei* Schneider and *C. barbatus* Garman**

No swimbladder was found in two adult fishes examined.

Family IDIACANTHIDAE***Idiacanthus fasciola* Peters**

No swimbladder was found in adult specimens.

Family MALACOSTEIDAE

No trace of a swimbladder could be found in adult *Malacosteus niger* Ayres and *Photostomias guernei* Collett.

Suborder SALMONOIDEA**Family OPISTHOPROCTIDAE*****Opisthoproctus soleatus* Vaillant (Text-fig. 14D)**

St. 3484, 39° 55' N., 20° 01' W., 1. x. 56, IKMT, 750(-0) m. Standard length 35 mm. (6.5 × 2.5 mm.).

The swimbladder of *Opisthoproctus*, which is ellipsoidal in form, lies above the stomach. When fully expanded it is evidently no less capacious an internal float than the swimbladder of a myctophid (of the same size).

Two blood-vessels enter the anterior end of the sac and then subdivide to form about twelve branches, which take more or less parallel courses within the swimbladder wall until they reach the gas-gland. Each of these vascular branches consists of from six to twelve closely associated capillaries, which are arranged in the form of a ribbon. In cross-section the ribbon consists of alternating arterial and venous capillaries (or arterioles and venules), the arterial elements having a diameter of about 12μ while the venous ones measure about 20μ . Clearly these are retial structures (see Text-fig. 14D), but they are quite unlike the massive retia of most teleosts with a closed swimbladder. Such elements might well be called micro-retia mirabilia.

These retia enter the gas-gland without subdividing and form capillary loops within the secretory tissue. The gland occupies a median region and entirely surrounds the sac. Beyond the gas-gland the walls consist of an inner epithelium and outer connective tissues. Perhaps it is here that resorption of gases takes place.

***Opisthoproctus grimaldii* Zugmayer (Text-fig. 14E)**

St. 1746, from $32^{\circ} 02.1' \text{ S.}$, $87^{\circ} 02.5' \text{ E.}$ to $31^{\circ} 56.6' \text{ S.}$, $86^{\circ} 55.1' \text{ E.}$, 22. iv. 36, D.R.R. 2513 m. Standard length 65 mm. (15.0×6.0 mm.).

Opisthoproctus grimaldii has a capacious swimbladder which is rounded anteriorly and tapers to a point at the other extremity. As in *O. soleatus*, blood-vessels enter the forward tip of the sac. There is a large vein that originates between the kidneys (presumably coming from the cardinal vein), while there are two arteries, one being a branch of the mesenteric system, the other running forward from the vessel to the ovaries.

Again, these vessels subdivide to form micro-retia, each composed of a ribbon of closely associated capillaries (from twelve to sixteen). The venous elements have a diameter of from 12 to 16μ , while their arterial counterparts measure from 8 to 10μ . At the forepart of the swimbladder there appeared to be about 30 micro-retia, these running backward to supply glandular patches, which seemed to be less concentrated than those of *O. soleatus*. However, they were most numerous over the middle part of the sac. These patches are formed of cells varying in size from about 30 to 150μ .

***Winteria telescopa* Brauer (Text-fig. 14A, B)**

St. 2066, $04^{\circ} 56.4' \text{ N.}$, $14^{\circ} 46.7' \text{ W.}$, 5. v. 37, N 450 B, 1550-0 m. Standard length 100 mm. (5.0×2.0 mm.).

The swimbladder of *Winteria* is suspended in the body-cavity just behind the stomach. In the above individual the sac is very relaxed, the walls being thick and having a nacreous appearance. From the posterior end of the swimbladder a long band of connective tissue runs backwards to an attachment on the right ovary.

An artery and vein enter the anterior end of the sac and subdivide into a number of smaller vessels, which run towards the gas-gland. This is found in the posterior half of the sac and seems to be a flattened oval structure lying on the floor of the swimbladder. However, the tissues are so shrunken that this may not be its true form. Running to the glandular area are at least twelve micro-retia composed of from eight to fourteen capillaries.

***Macropinna microstoma* Chapman**

Chapman (1942b) was unable to find a swimbladder in this species.

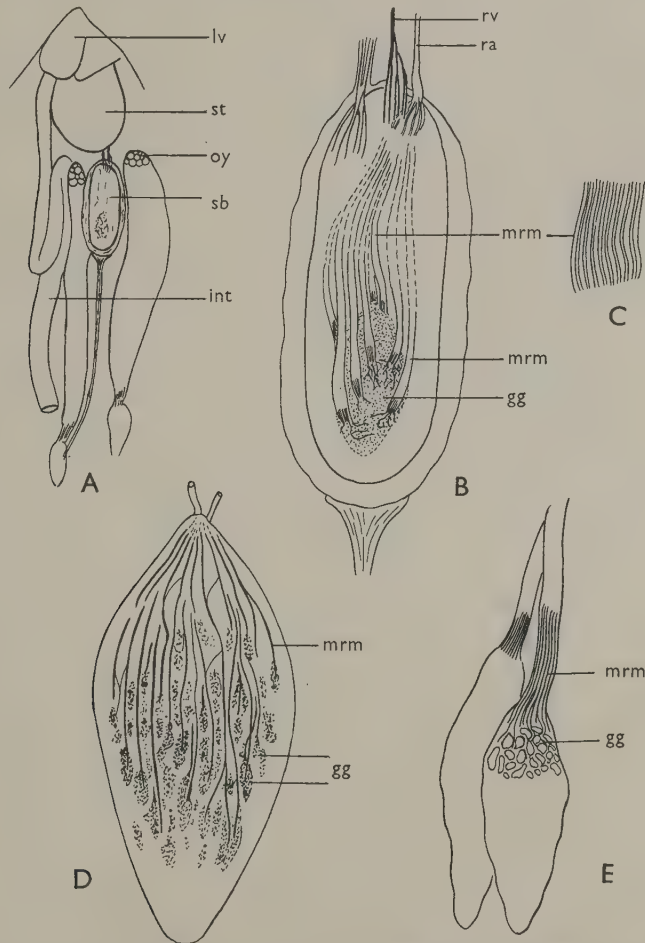
Family MICROSTOMIDAE

***Xenopthalmichthys danae* Regan**

Bertelsen (1958) records that the swimbladder is absent.

A well-developed swimbladder is found in the genera *Argentina*, *Glossanodon*, *Microstoma* and *Nansenia* (Cohen, 1958; Fänge, 1958, and personal observation). Fänge's description of the swimbladder of *Argentina silus* shows that micro-retia are also present in another deep-sea salmonoid and that the system is highly developed. I have also found an extensive development of micro-retia in *Microstoma* and *Nansenia*. However, as these four genera appear to consist of benthic fishes they are not considered here. Further discussion may be found in the section on pages 53-54.

The swimbladders of the two species of *Opisthoproctus* and *Winteria telescopa* were not sufficiently well preserved to trace the resorbent capillary network. However, it is likely to be found at the posterior end of the sac. This is certainly true of *Argentina* and *Microstoma*, in which this part is thin walled and carries a capillary bed (see also pp. 79-80).



Text-fig. 14. Swimbladders of *Winteria telescopa* (A and B) and *Opisthoproctus soleatus* (D), seen from below. In (C) part of a micro-rete of *Winteria* is seen and in (E) two micro-retia of *Opisthoproctus grimaldii*, which supply patches of gas-gland. gg, gas-gland; int, intestine; lv, liver; mrm, micro-rete mirabile; oy, ovary; ra, retial artery; rv, retial vein; sb, swimbladder; st, stomach. (A, $\times 3.5$; B, $\times 12.5$; C, $\times 60$; D, $\times 10$; E, $\times 60$.)

Family BATHYLAGIDAE

In his synopsis of this family, Chapman (1943) recorded that the swimbladder is completely absent. Beebe (1933), who examined the internal organs of *Bathylagus benedicti* and *B. glacialis*, made no mention of this organ, while I could find no trace of it in *B. antarcticus* and *B. argyrogaster*.

Suborder CLUPEOIDEA

Family ALEPOCEPHALIDAE

Alcock (1899) stated that the Alepocephalidae have no swimbladder. Beebe (1933) examined the internal organs of *Bathytroctes rostratus* and *Xenodermichthys copei*, but made no mention of a swimbladder. I was unable to find any trace of this organ in an adult of the latter species, nor in *Searsia koefoedi*.

Order INIOMI

Suborder MYCTOPHOIDEA

Family MYCTOPHIDAE

Myctophum punctatum Rafinesque (Text-fig. 15A-C)

St. 3233, 46° 02' N., 09° 19' W., NH, 0 m. Standard lengths of fishes 74.5, 71.0, 69.0 and 59.0 mm.

In this lantern fish a capacious swimbladder is found above the stomach. The anterior end is opposite the margins of the gill-covers, while the posterior extremity lies under the origin of the dorsal fin. The sac is thin-walled and ellipsoidal in form, the major and minor axis measuring 11.0 and 4.5 mm. in the 69.0-mm. fish.

Three retia mirabilia are found on the underside of the forward, rounded end of the sac. The retial blood supply comes from an artery running backwards and downwards from the dorsal aorta and returns through a vein that joins the hepatic portal system.

In the 74.5-mm. fish, each of the three retia mirabilia (which have a length of about 2 mm.) runs to a corresponding lobe of the gas-gland. The middle lobe is shaped rather like a rose petal and lies over the floor, while the left and right lobes, which are fan-like, extend over the lateral walls. As in all lantern fishes, the surface of the gland has a convoluted appearance, due to the meanderings of the capillary loops with their associated investments of gland cells. This kind of rete in which the arterial and venous capillaries run straight to the gas-gland without forming larger vessels is termed unipolar.

Above the retia mirabilia is a resorbent 'oval' which is partly expanded. It measured 2.5 mm. along the longitudinal axis and 2.2 mm. in width. The oval bears a fine-meshed network of capillaries fed by two branches of the retial artery. The venous return is through a large vessel running upwards and forwards to a point between the kidneys, presumably to the posterior cardinal vein.

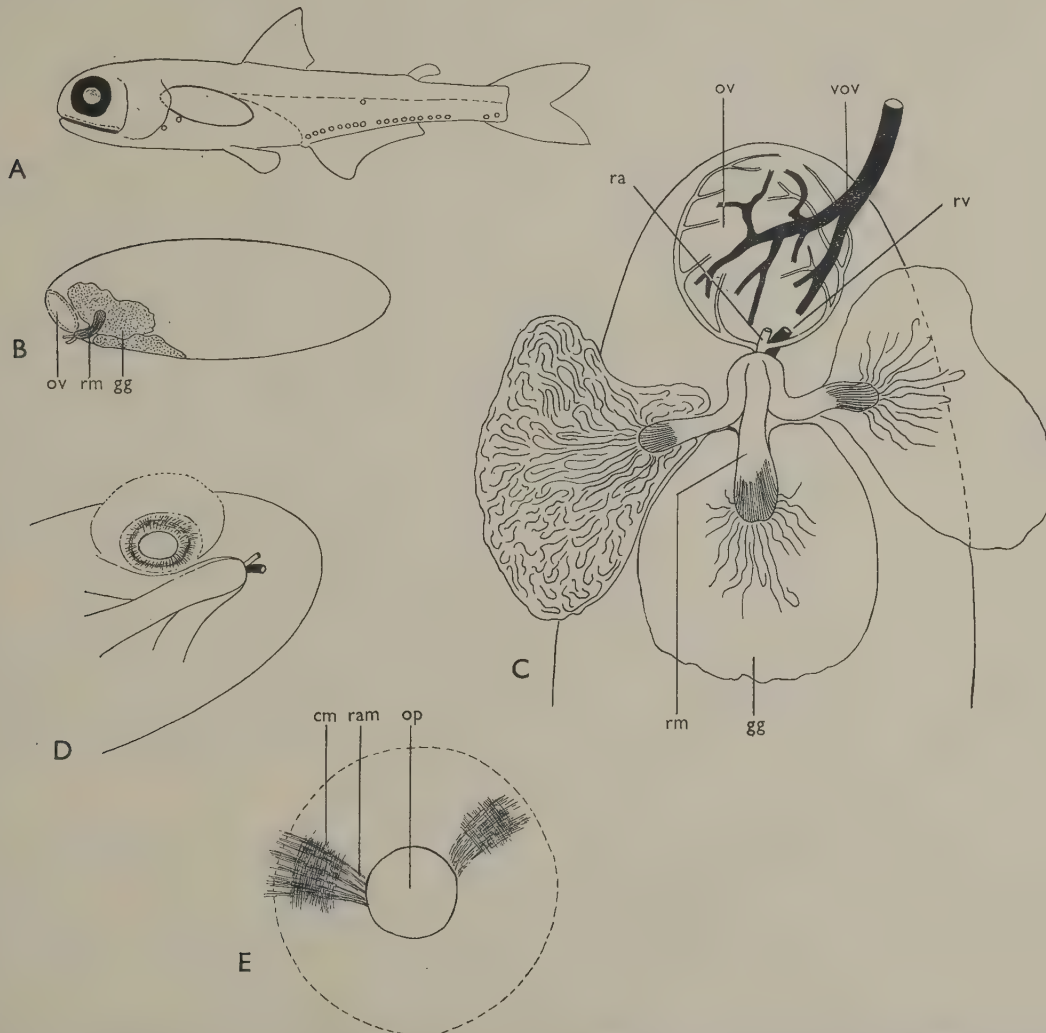
In the 69-mm. fish the oval is partly expanded and the opening into the swimbladder has a diameter of 2.5 mm. The capillary-bearing tissue is an egg-shaped blister measuring 3.5 along the longitudinal axis and 3.0 mm. in greatest width. The oval of the 59-mm. fish is shut, the inner surfaces of the walls being thrown into folds. The fine structure of the oval in the closed phase will be dealt with in more detail in a later section (p. 80).

Diaphus rafinesquei (Cocco) (Text-fig. 15D, E)

St. 3484, 39° 55' N., 20° 01' W., I. X. 56, IKMT, 750(-0) m. Standard length 70 mm.

A detailed description of the swimbladder of this myctophid has been given by Rauther (1922). According to his reconstruction of transverse sections (shown in his fig. 13), the swimbladder of his fish measured about 7 mm. in total length. The middle depth was rather less than 1 mm. In the Discovery fish the length of the sac is about 20 mm. and the middle depth about 7 mm. Rauther showed the walls of the swimbladder to be relatively thick, but the sac was clearly not in an expanded condition. There was an outer fibrous layer which did not cover the roof, and then came two layers of loose and closely packed connective tissue fibres.

Continuing Rauther's description, the inner epithelial layer forms an extensive gas-gland covering most of the floor and side walls of the swimbladder, and also the roof of the anterior part. There are three retia mirabilia supplied by an artery that joins the dorsal aorta close to the coeliac artery, while the venous return is through a vessel opening into the portal system. The left rete extends upwards to the roofing part of the gas-gland, while the middle and right retia supply the remaining glandular area. Measured from Rauther's fig. 13 the lengths of the retia, in the order just mentioned, are about 2.5–3.0 mm.



Text-fig. 15. Swimbladder of *Myctophum punctatum*, seen (A) in position in body-cavity of fish, (B) laterally, (C) ventrally (anterior part of organ). The oval of *Diaphus rafinesquei* is shown in Text-figs. 15D and E. *cm*, circular muscle of oval; *ram*, radial muscle of oval; *gg*, gas-gland; *op*, opening from oval into swimbladder chamber; *ov*, oval; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *vov*, vein to oval. Veins shown black, arteries white. (A, $\times 1$; B, $\times 5$; C, $\times 12$; D, $\times 7$; E, $\times 15$.)

There is an anterior chamber, called by Rauther the praesvesica, opening into the right side of the main sac just behind its forward tip. The chamber has an outer fibrous layer and an inner much-folded layer of loose connective tissue containing a capillary network. Rauther remarked that this blood-system was like that he found in the respiratory part of the swimbladder of the mud-minnow,

Umbra. The arterial supply for the network comes from the retial artery, while there is a vein running forward and upwards from the chamber to the cardinal (?) vein.

Examination of the Discovery fish revealed that Rauther's 'praevesica' is no more than a very distorted oval. In this fish the oval lies immediately to the right of the retia mirabilia and the capillary bearing surface is blown out in the form of a blister, due no doubt to the release of pressure as the fish was hauled to the surface. Had sections been cut of this structure, it would also have looked like an anterior chamber. At the base of the oval is a circular aperture with a diameter of about 0.75 mm. which opens into the main cavity. From the rim of this opening radial muscles extend outwards and are crossed by a complex of circular muscle fibres. Clearly the whole structure conforms to that of the oval found in some fishes with a closed swimbladder, much like that described in the perch (*Perca fluviatilis*) by Saupe (1939).

Like *Myctophum punctatum* and *Diaphus rafinesquei*, each of the other lantern fishes dissected has an ellipsoidal swimbladder provided with three unipolar retia mirabilia. The gas-gland is three-lobed, each lobe receiving a corresponding rete. An oval is also present.¹ In view of this, the descriptions which follow will be confined to the more significant features. Immediately after the length of the fish, measurements of the major and minor axes of the swimbladder appear in parenthesis.

***Electrona tenisoni* (Norman) (Text-fig. 16D-F)**

St. 2023, 50° 17.7' S., 00° 23.1' E., 28. iii. 37, N 100 B, 750-400(-0) m. B.M. Reg. no. 1948. 5.14.16. Standard length 47.0 mm. (4.5 × 1.5 mm.).

The swimbladder of this fish is well developed, although this is hardly revealed by the dimensions of the sac, which is much contracted. Three retia, almost 2.5 mm. in length, enter the anterior floor to supply a heart-shaped gas-gland. The bunched-up appearance of the gland, which covers much of the floor, also reveals the collapsed state of the organ.

Towards the base of the retia, but more to the right side of the sac, is the oval, with wrinkled outer walls. The inner tissues lining the wall are folded and ridged, and bear a network of blood capillaries. The structure is almost closed, there being but a small opening (about 0.5 mm. in diameter) communicating with the main lumen of the swimbladder. The blood-supply consists of two branches from the retial artery and a large vein, which runs forward and upward to the cardinal vein between the kidneys.

***Electrona rissoi* (Cocco)**

St. 101, 33° 50' to 34° 13' S., 16° 04' to 15° 49' E., N 450, 400-350(-0) m. B.M. Reg. no. 1930.1.12. 597-8. Standard length 61 mm. (12 × 4 mm.).

This species has a capacious swimbladder occupying about three-quarters the length of the body-cavity. On the right of the sac and just behind the anterior tip is the oval, which receives a large vein and a number of small branches coming from the retial artery. The organ is almost closed, the walls having a much folded appearance. Around the opening into the main cavity of the swimbladder are circular and radial muscles.

***Electrona antarctica* (Günther) (Text-fig. 16A-C)**

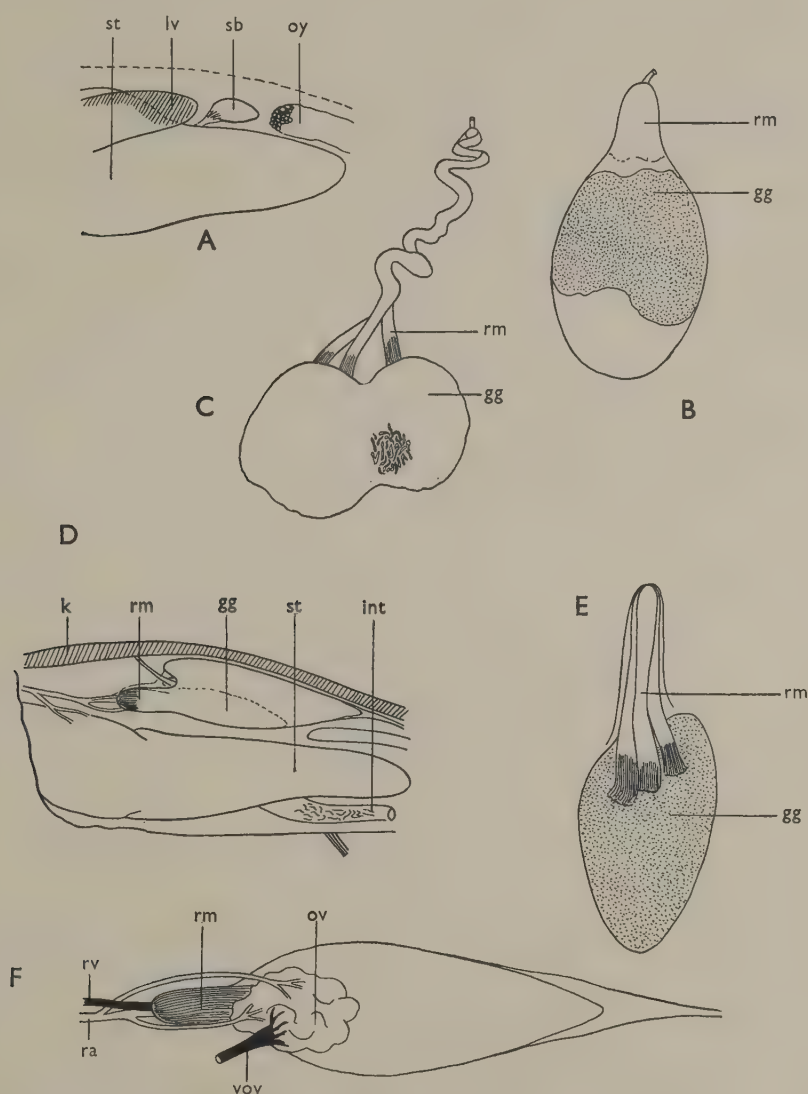
St. 114, 52° 25' 00" S., 9° 50' 00" E., 12. xi. 26, N 450, 650-700(-0) m. B.M. Reg. no. 1930.1.30. 622-7. Standard lengths of two fishes examined, 26.0 and 59.0 mm.

St. 2535, 52° 40.8' S., 02° 45.4' E., 16. i. 39, N 100 B, 1050-0 m. Standard length 36 mm.

In all three fishes the swimbladder is oval in outline and is suspended in the body-cavity over the forward half of the stomach. The sac of the smallest specimen measured a little more than 3 mm. in

¹ The part of the swimbladder serving for gas-resorption.

length and 3 mm. in greatest width. The retia mirabilia are contained in a conical projection at the anterior end, and they are wound spirally round one another. When opened out, three long retia were revealed, each about 5 mm. in length, these running to a gas-gland covering about three-quarters of the swimbladder floor.



Text-fig. 16. Swimbladders of *Electrona antarctica* (A, B and C) and *E. tenisoni* (D, E and F). B, C, E and F are ventral views. gg, gas-gland; int, intestine; k, kidney; lv, liver; ov, oval; oy, ovary; ra, retial artery; rv, retial vein; rm, rete mirabile; sb, swimbladder; st, stomach; vov, vein to oval. (A, $\times 3.5$; B, $\times 15$; C, $\times 17.5$; D, $\times 6$; E, $\times 18$; F, $\times 14$.)

The fish from St. 2535 has a rather larger swimbladder measuring nearly 4 mm. in length. In this, the arterial supply for the retia mirabilia came from the coeliaco-mesenteric vessel. The walls of the bladder were quite thin.

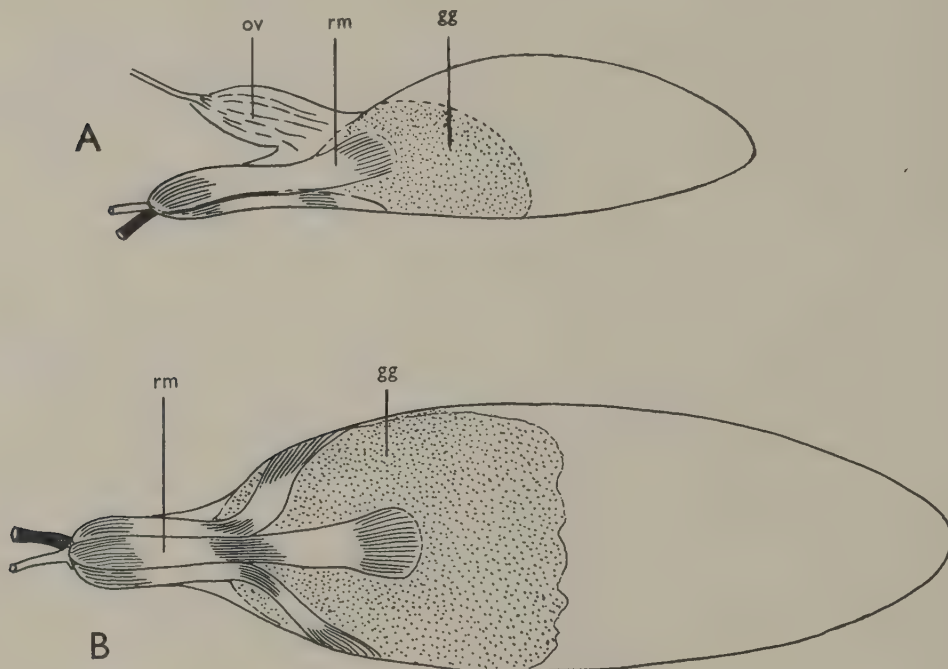
Finally, the swimbladder of the 59-mm. fish measured no more than 2.0 and 1.2 mm. across the major and minor axes. It is clear that the organ regresses during the adult phase.

***Hygophum benoiti* (Cocco) (Text-fig. 17)**

B.M. Reg. no. 85.6.22. 120-9. Straits of Messina. Standard length 4.1 mm. (7.0 × 2.0 mm.).

The swimbladder of this lantern fish is both thin-walled and capacious. At the anterior end three retia mirabilia run into the gas-gland, which covers most of the floor and side walls of the forward half of the organ. Each rete has a length of nearly 3.0 mm.

Over the point of entry of the retia mirabilia into the gas-gland and rather to the right of the swimbladder is a forward conical extension (the distorted oval) receiving a rich supply of blood-vessels. Within the oval the walls are thrown into a series of longitudinal ridges.



Text-fig. 17. Swimbladder of *Hygophum benoiti*, seen (A) laterally, and (B) ventrally. *gg*, gas-gland; *ov*, oval; *rm*, rete mirabile. (A, × 13.5; B, × 19.)

***Benthoosema glaciale* (Reinhardt) (Text-fig. 18D-F)**

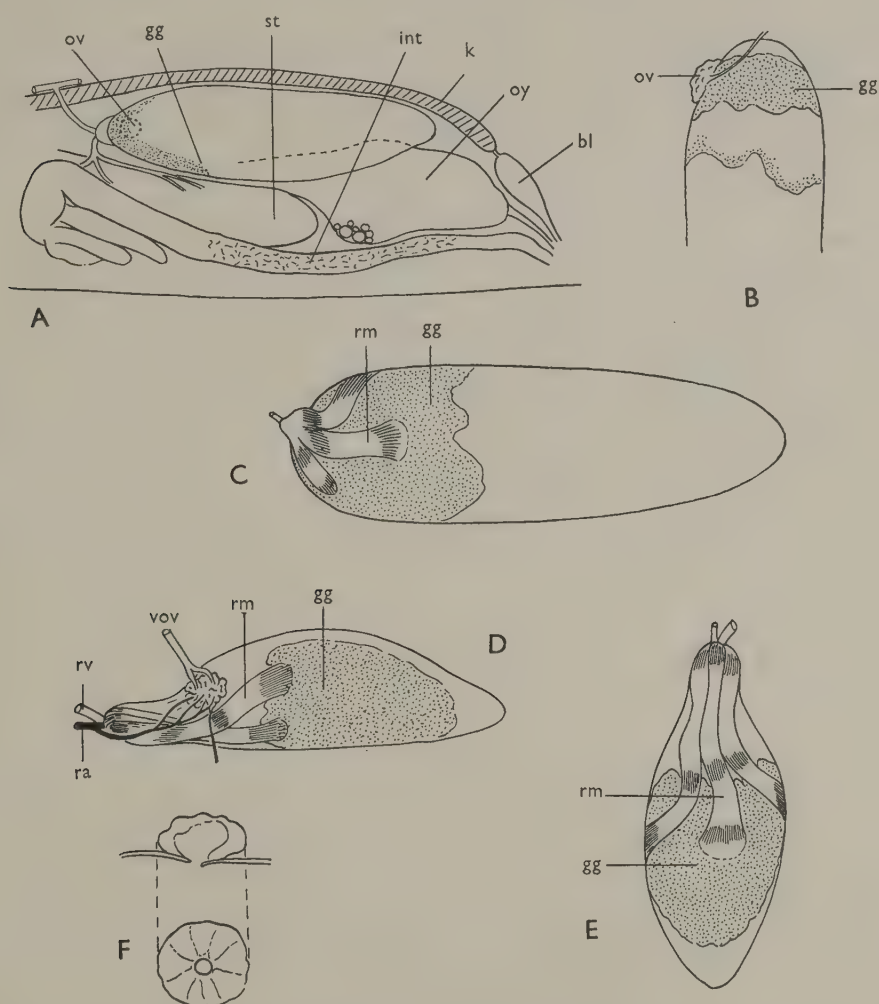
Position, 13° 25' N., 18° 22' W., 28. x. 25, N 450 V, 900(-0) m. B.M. Reg. no. 1930.1.12. 641-7. Standard length of fish 45.5 mm. B.M. Reg. no. 1911.2.8. 3-12. Between Faroes and S.W. Ireland. Standard length of fish 58-5 mm.

The swimbladder of this myctophid is thin walled and lies above the stomach. In the 45.5 mm. fish it measured 5.5 mm. in length and about 2 mm. in depth and width at the middle region. A bulbous projection at the fore-end of the bladder contains the three retia mirabilia, which run backwards to a gas-gland investing much of the floor and side walls. Each rete has a mean length of about 3 mm., the two outer systems being rather longer than the middle.

Just behind the base of the bulbous forward projection and on the left-hand side of the swimbladder is a small rounded chamber (the oval) receiving many blood-vessels. The oval has a sphincter-controlled opening into the main cavity, while the walls are thrown into radially disposed folds. In the

Discovery fish the chamber was about 0.5 mm. in diameter and the inner opening, which was oval, measured 0.5×0.3 mm. The corresponding figures for the other fish are 0.6 and 0.2×0.2 mm.

In both fishes the anterior part of the swimbladder was entirely invested by fatty tissue, which extended under the organ (and beyond it in the larger individual).



Text-fig. 18. Swimbladders of *Benthosema suborbitale* (A, B, C), and *B. glaciale* (D-F). A, C, D, E, lateral views; B, dorsal view. The almost closed oval of *B. glaciale* is seen in diagrammatic transverse section and from below in (F). *bl*, urinary bladder; *gg*, gas-gland; *int*, intestine; *k*, kidney; *ov*, oval; *oy*, ovary; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *st*, stomach; *vov*, vein to oval. (A, $\times 11.5$; B, $\times 15$; C, $\times 15$; D, $\times 11$; E, $\times 10$; F, $\times 20$.)

Benthosema suborbitale (Gilbert) (Text-fig. 18A-C)

St. 2067, $24^{\circ} 12' N.$, $21^{\circ} 12.2' W.$, 12. v. 37, N 450 H, 68(-0) m. B.M. Reg. no. 1948.5.14. 185-91. Standard length of fish 24 mm. (4.3×1.3 mm.).

A thin-walled swimbladder originates over the forepart of the stomach and extends over some two-thirds of the length of the body-cavity.

The gas-gland invests the floor of the foremost third of the organ. As in all myctophids, the gland receives three retia mirabilia, which enter the anterior and lower part of the swimbladder.

Not far behind the forward tip and on the right-hand side of the bladder, the oval, which is almost closed, appears as a small circular blister, about 0.3 mm. in diameter. This has a small opening into the main cavity and the much folded walls have a rich supply of blood capillaries.

***Diogenichthys atlanticus* (Tåning)**

St. 288, 00° 56' 00" S., 14° 08' 30" W., 21. viii. 27, TYF, 250(-0) m. B.M. Reg. no. 1930.1.12. 846-7. Standard length 25.5 mm. (3.0 × 0.6 mm.).

The swimbladder of this specimen was in a relaxed state, the walls appearing thicker than they would be when the sac is inflated. The three retia mirabilia are bound together in a bulbous forward extension and are closely followed by the gas-gland, which covers about three quarters of the swimbladder floor.

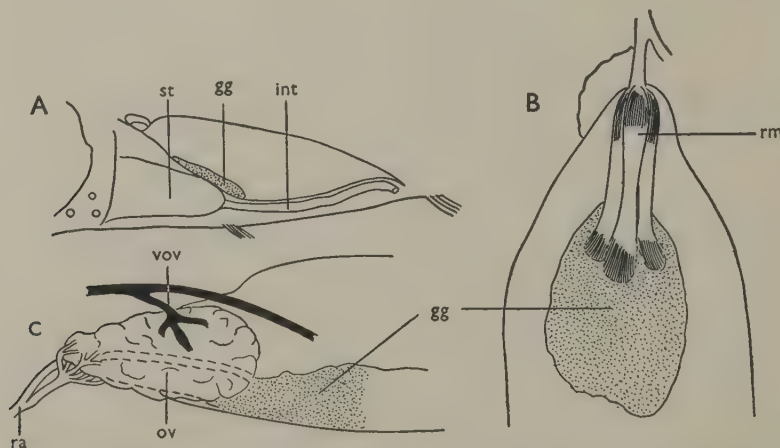
***Myctophum humboldti* (Risso)**

St 1566, 40° 42' S, 36° 05.5' E., 9. iv. 35, N 70 H, 0-5 m. Standard length 50 mm. (8.0 × 4.0 mm.).

This species has a capacious thin-walled swimbladder. The three retia mirabilia run underneath the forward, rounded end of the swimbladder to the gas-gland, which is three lobed and extends over the floor and lateral walls. Each rete is about 3 mm. in length, while the gas-gland has a length of about 2.5 mm. and a width (when flattened out) of about 4.5 mm.

***Myctophum affine* (Lütken) (Text-fig. 19)**

St. 694, 04° 05½' N., 30° 00' W., 10. v. 31, NH, 0 m. B.M. Reg. no. 1948.5.14. 234-6. Standard length 51 mm. (9.0 × 4.0 mm.).



Text-fig. 19. Swimbladder of *Myctophum affine*, seen (A) in body-cavity, (B) ventrally (anterior end), and (C) laterally (anterior end). gg, gas-gland; int, intestine; ov, oval; ra, retial artery; rm, rete mirabile; st, stomach; vov, vein to oval. (A, × 4.5; B, × 25; C, × 25.)

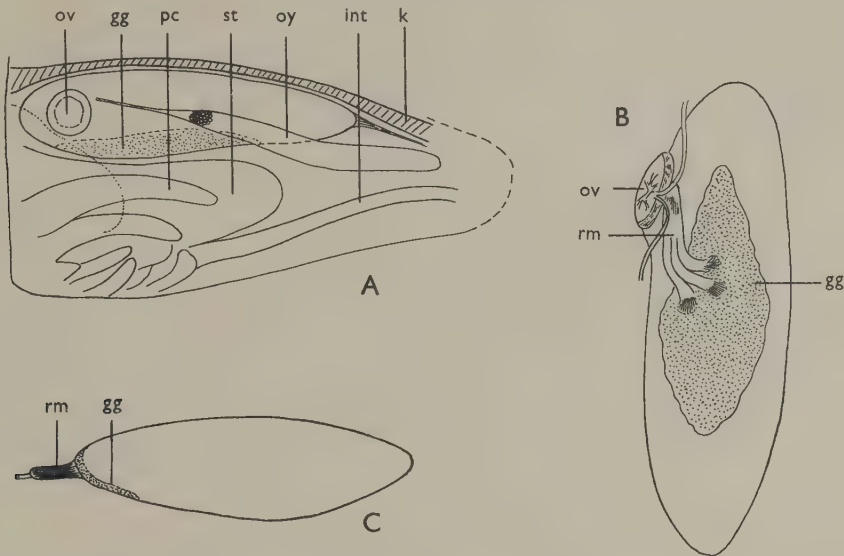
The swimbladder is thin walled and extends down some three-quarters of the length of the body-cavity. The retia mirabilia extend back from the foremost tip of the sac and run to an oval-shaped gas-gland lying on the floor of the anterior half. The gland measured 1.5 mm. in length and 1.25 mm. in width, while the retia spanned about 1.5 mm.

To the left of the forward end of the swimbladder is the oval, which is closed, and appears as a wrinkled projection with thick, expanded walls.

Diaphus dofleini Zugmayer (Text-fig. 20A, B)

St. 250, 36° 09' 00" S., 5° 33' 00" W., 17. vi. 27, TYF, 300(-0) m. B.M. Reg. no. 1930.1.12. 831-2. Standard length 32 mm. (6.5 × 1.5 mm.).

This lantern fish has a thin-walled swimbladder, which originates over the forepart of the stomach and spans nearly two-thirds the length of the body-cavity. The retia mirabilia arise to the right of the lower surface of the sac, about 1 mm. behind its forward end. Each rete is nearly 1.5 mm. in length. The three lobes of the gas-gland, which invest the middle part of the swimbladder floor, are roughly oval in outline and measure 2.5 and 1 mm. in length and breadth.



Text-fig. 20. Swimbladders of *Diaphus dofleini* (A and B) and *D. garmani* (C). A and C are lateral views; B is a ventral view. gg, gas-gland; int, intestine; k, kidney; ov, oval; oy, ovary; pc, pyloric caecum; rm, rete mirabile; st, stomach. (A, × 8; B, × 10; C, × 8.5.)

Just above the point of origin of the retia and on the right side of the sac, the oval appears as a circular cap (about 0.75 mm. in diameter). It is partly open, the capillary-bearing part being surrounded by a ring of connective tissue containing circular and radial muscle fibres.

Diaphus garmani Gilbert (Text-fig. 20C)

B.M. Reg. no. 1934.5.4. 1-2. Montserrat. Standard length 34.5 mm. (6.0 × 2.0 mm.).

A thin-walled swimbladder was found just above the stomach. The three retia mirabilia are bound together in a club-shaped forward extension of the swimbladder. They are about 1 mm. in length and supply a rather small gas-gland. This extends over the floor and lateral walls of the foremost quarter of the organ.

Diaphus luetkeni (Brauer)

St. 288, 00° 56' 00" S., 14° 08' 30" W., 21. viii. 27, TYF, 250(-0) m. B.M. Reg. no. 1930.1.12. 846-7. Standard length 34 mm. (3.5 × 1.2 mm.).

As the swimbladder of this fish was relaxed, the walls appear thick, while the gas-gland occupies most of the floor. When the sac is expanded, the dimensions must be considerably more than those given above.

Standard length 54 mm.

***Diaphus agassizii* Gilbert**

This individual contained a well-developed swimbladder measuring about 7 mm. in length.

***Notolychnus valdiviae* (Brauer) (Text-fig. 21D)**

St. 1586, 02° 39' 4" N., 50° 46' 4" E., 2. v. 35, TYFB 1650-950(-0) m. B.M. Reg. no. 1948.5.14. 310-25. Standard length 19 mm. (1.5 × 0.75 mm.).

As in other myctophids, the swimbladder originates over the stomach, but is so small that it does not extend beyond this organ. Except for the roof, the gas-gland covers the entire inner surface of the sac. The three retia mirabilia, which have a length of about 1.75 mm., run backwards and upwards along the right lateral wall of the stomach and enter the anterior part of the swimbladder floor.

In another fish (standard length 19.5 mm.) from St. 1586 the swimbladder had a length of nearly 2.5 mm. Though the sac of both fishes was somewhat relaxed, it would seem that the swimbladder of this species is reduced in size.

***Lampadena chavesi* Collett (Text-fig. 21A-C)**

Position, 51° 23' N., 11° 47' W. B.M. Reg. no. 1911.2.8. 1. Standard length 75 mm. (9.5 × 3.5 mm.).

The swimbladder of this lantern fish arises above the forepart of the stomach and extends down the remainder of the body-cavity. The three retia mirabilia enter the right anterior part of the sac and run backwards to supply a gas-gland covering the forward half of the swimbladder floor.

Each rete has an individual length. The innermost one, with a span of about 2.5 mm. supplies the foremost lobe of the gas-gland, while the next lobe is fed by the middle complex, which is 4.5 mm. in extent. The outermost rete is the largest (about 5.75 mm.) and runs to the posterior lobe of the gland.

Alongside the retia, forming an anterior extension of the swimbladder, is a conical projection (presumably the oval) that is well supplied with blood-vessels.

***Lampanyctus guntheri* Goode & Bean (Text-fig. 22A)**

St. 710, 21° 45' S., 39° 50' W., 26. x. 31, TYFB, 294(-0) m. B.M. Reg. no. 1948.5.14. 534-56. Standard length 53 mm. (9.5 × 2.5 mm.).

In this species the swimbladder is a thin-walled sac occupying about four-fifths the span of the body-cavity. The rounded forward extremity lies just behind a vertical line drawn through the base of the pectoral fins.

The three retia mirabilia lie under the forepart of the swimbladder and extend backward to the medially situated gas-gland. Each rete is almost 3 mm. in length, while the gas-gland, which invests the floor and side walls, has a length of 2.3 mm. The artery and vein supplying the retia mirabilia come from the dorsal aorta and hepatic portal system respectively.

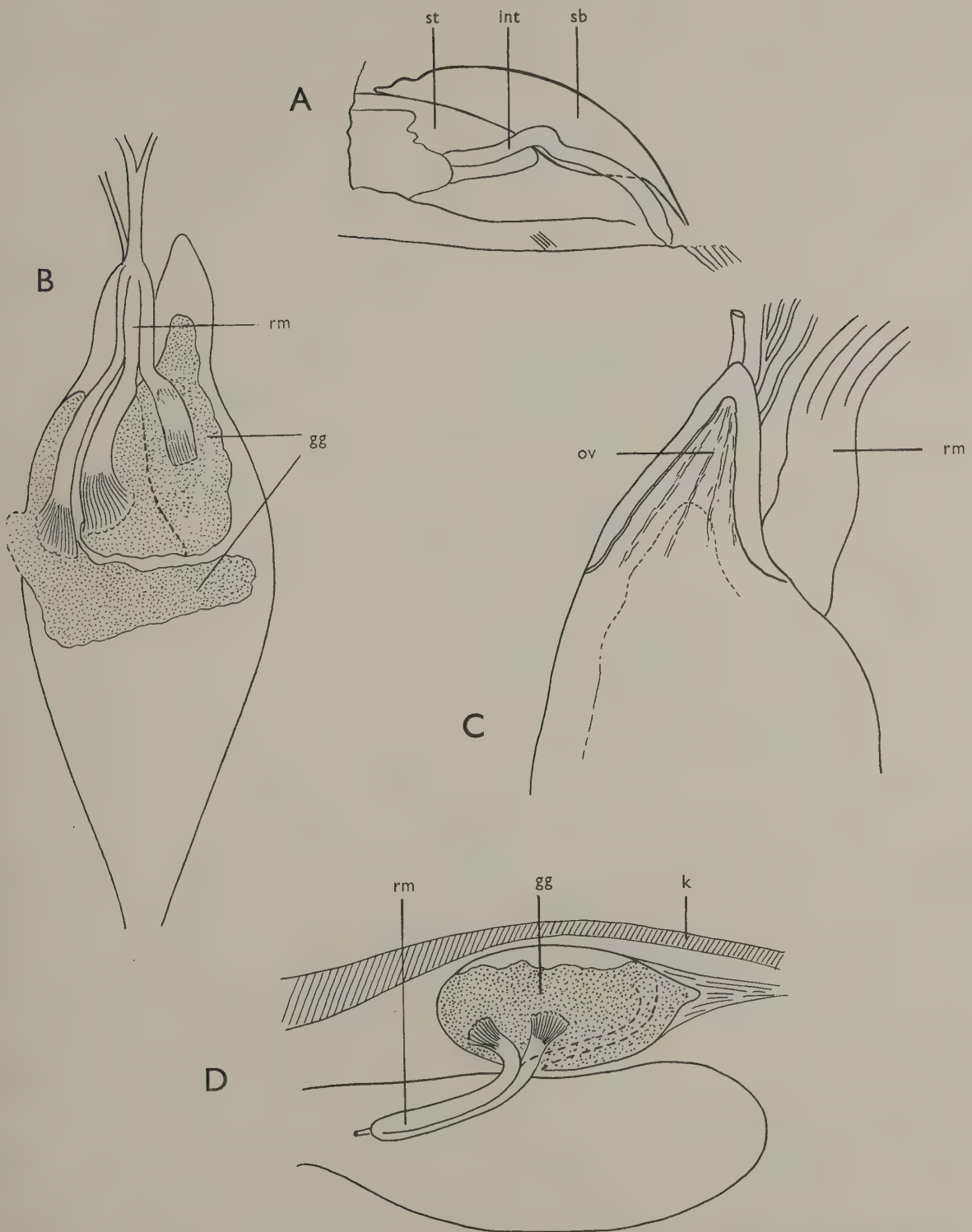
Centred above the middle point of the retia and on the left side of the swimbladder, the oval appears as a thin-walled blister, 1.8 mm. in width. This opens into the main cavity through an oval aperture situated in the side wall just above the retia. The walls of the oval are richly supplied with capillaries and larger vessels.

***Lampanyctus alatus* Goode & Bean (Text-fig. 22B)**

St. 2057, 12° 09' S., 04° 28' 2" W., 29. iv. 37, N 450 B, 1450-700(-0) m. B.M. Reg. no. 1948.5.14. Standard length 57.0 mm. (9.0 × 2.5 mm.).

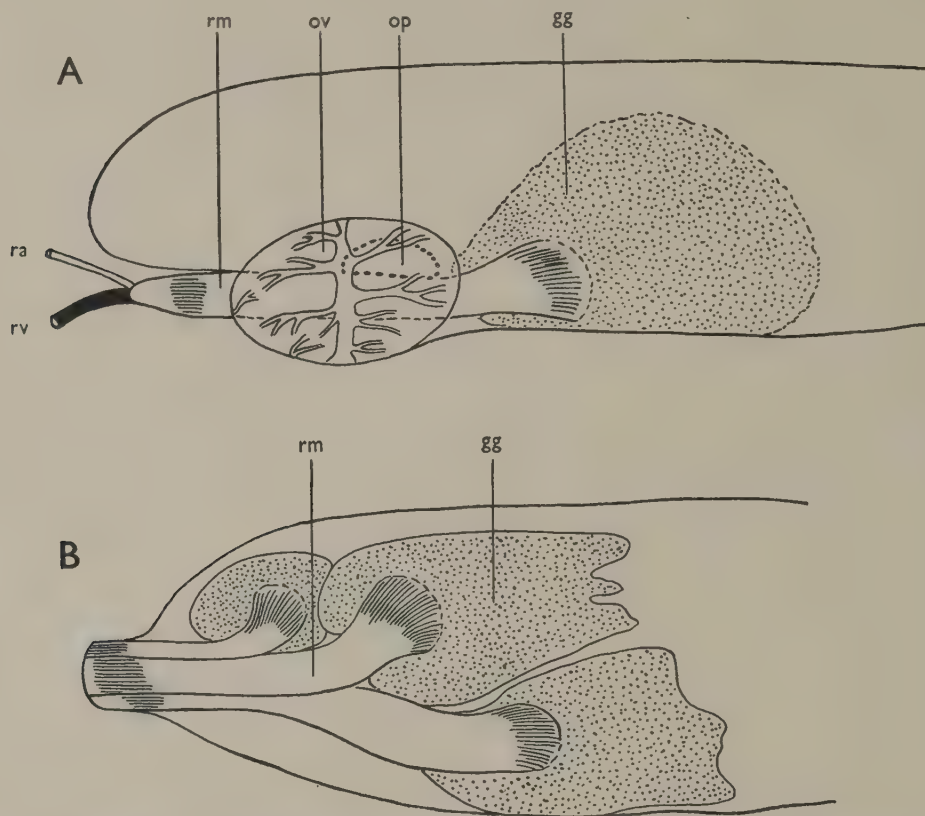
This species has a capacious swimbladder extending down about two-thirds the length of the body-cavity. The walls are rather thin but well strengthened, with collagen fibres.

In side view the swimbladder has a gradually tapering forward section, the floor of which is



Text-fig. 21. Swimbladders of *Lampadena chavesi* (A) in body-cavity; (B) ventral view; (C) dorsal view (anterior end), and (D) *Notolychnus valdiviae*, lateral view. gg, gas-gland; int, intestine; k, kidney; ov, oval; rm, rete mirabile; sb, swimbladder; st, stomach. (A, $\times 6.9$; B, $\times 9.9$; C, $\times 18.9$; D, $\times 30$.)

covered by the gas-gland. This has three lobes, each receiving a rete mirabile. The retia originate in front of the sac, and are bound together to form a cylindrical structure, before diverging over the under surface of the gas-gland. The left, middle and right retia have lengths of about 2.5, 3.0 and 4.0 mm. respectively, differences parallel to those found in *Lampadena chavesi*.



Text-fig. 22. Swimbladders of *Lampanyctus guentheri* (A) lateral view of anterior half, and *L. alatus* (B), ventral view of anterior half. gg, gas-gland; op, opening of oval into main cavity of swimbladder; ov, oval; ra, retial artery; rv, retial vein; rm, rete mirabile. (A, $\times 27$; B, $\times 22.5$.)

Lampanyctus pusillus (Johnson)

St. 1602, $17^{\circ} 59.9' \text{ S.}$, $04^{\circ} 27.1' \text{ E.}$, 27. x. 35, TYFB, 175(-) m. B.M. Reg. no. 1948.5.14. 389-91. Standard length 22 mm. ($3.0 \times 0.5 \text{ mm.}$).

St. 100 C, $33^{\circ} 20' - 33^{\circ} 46' \text{ S.}$, $15^{\circ} 18' - 15^{\circ} 08' \text{ E.}$ 4. x. 26, TYF, 2500-2000(-) m. B.M. Reg. no. 1930.1.12. 762-3. Standard length 33 mm. ($6.5 \times 1.5 \text{ mm.}$).

The swimbladder of this species lies over the posterior half of the stomach and extends beyond it as far as the level of insertion of the pelvic fins. In both specimens the sac is considerably relaxed.

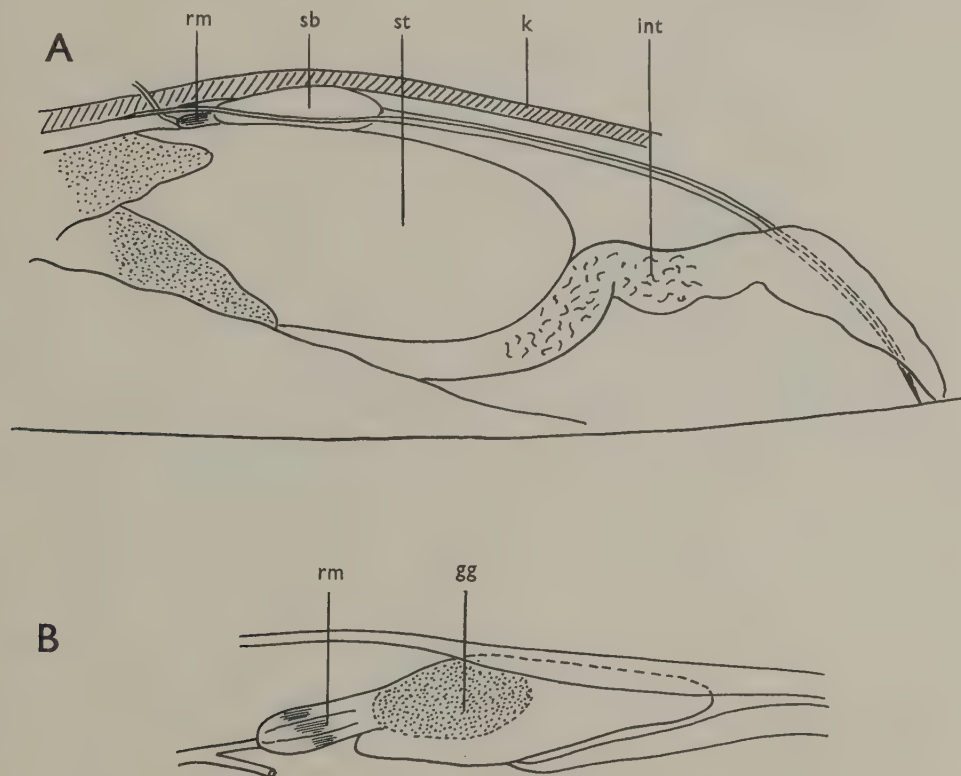
The retia mirabilia originate to the left of the anterior tip of the swimbladder and extend backwards to the gas-gland, which covers the forward part of the floor. Close examination of the 33-mm. fish revealed that each rete has a different length. The inner one supplies an anterior lobe of the gas-gland, the middle one a middle lobe and the outer one a posterior lobe. Their lengths in the order given are 3.0, 2.3 and 1.8 mm.

An oval is present on the roof of the sac above the forward part of the retia.

Gymnoscopelus nicholsi (Gilbert) (Text-fig. 23)

St. WS 213, 49° 22' S., 60° 10' W., 30 v. 28, N 4-T, 249-259 m. B.M. Reg. no. 1948.5.14. 621-6. Standard length 50 mm.

The swimbladder, which is found over the middle region of the stomach, measured no more than 2.5 mm. in length. As in all myctophids, three retia mirabilia, which are closely bound together, enter the anterior end of the swimbladder. The gas-gland is oval in outline and invests the floor of the swimbladder over its anterior half. The walls of the bladder are so thick that little remains of the inner cavity. Clearly, the organ has undergone considerable regression.



Text-fig. 23. Swimbladder of *Gymnoscopelus nicholsi* (A) seen in position in body-cavity, and (B) ventral view. *gg*, gas-gland; *int*, intestine; *k*, kidney; *rm*, rete mirabile; *sb*, swimbladder; *st*, stomach. (A, $\times 12$; B, $\times 22.5$).

Ceratoscopelus townsendi (Eigenmann & Eigenmann)

St. 703, 10° 59' 3" N., 27° 03' 8" W., 17. x. 31, TYFB, 358-0 m. B.M. Reg. no. 1948.5.14. 584-5. Standard length 55.0 mm. (5.5 $\times$ 1.5 mm.).

Being in a rather relaxed condition, the swimbladder of this fish did not extend beyond the pyloric end of the stomach. The three retia mirabilia enter the floor of the sac at its forward end to supply a gas-gland that extends from one extremity to the other. However, when the sac is expanded conditions may well be different.

Opposite the point of entry of the retia is the oval, which has the appearance of a collapsed blister. The capillary network is fed through a vessel from the retial artery, while the return circulation is by way of a large vein running upwards to the roof of the body-cavity.

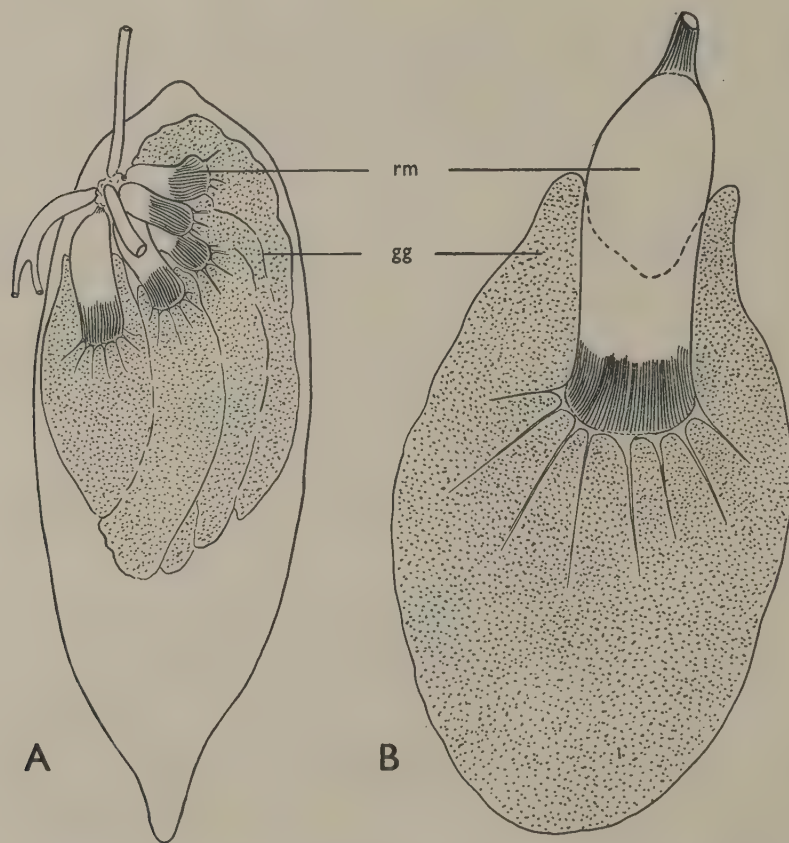
No trace of a swimbladder was found in adults of the following species: *Gonichthys coccoi* (Cocco), *Ctenobranchus nigro-ocellatus* (Günther), *Diaphus coeruleus* Klunzinger, and *Gymnoscopelus braueri* (Lönnberg).

Family NEOSCOPELIDAE

Neoscopelus macrolepidotus Johnson (Text-fig. 24)

John Murray Expedition St. 145, Maldives Area, 494 m. B.M. Reg. no. 1939.5.24. 475-84. Standard length 118 mm. (30.0 × 10.0 mm.).

A capacious swimbladder with rounded anterior and tapering posterior extremities runs down the greater part of the upper body-cavity. The lower half of the sac, which is rather thick walled, is invested with pigmented peritoneum.



Text-fig. 24. Swimbladder of *Neoscopelus macrolepidotus*, seen (A) from below. In (B) is shown a single rete and lobe of the gas-gland. gg, gas-gland; rm, rete mirabile. (A, × 3.9; B, × 9.3.)

The gas-gland covers some two-thirds of the floor of the sac and is fed by five massive retia mirabilia. These originate from a blood-vessel junction, which is found on the right-hand side of the anterior under-surface of the swimbladder. The junction receives a large vein from the hepatic portal system and an artery from the system of vessels on the roof of the stomach. There is also a blood-vessel (probably an artery) running backwards to the junction from the forward end of the swimbladder. But the fish is so poorly preserved that it is impossible to trace the blood-system with any certainty.

A careful search was made for the resorptive part of the swimbladder. No trace of an oval could be seen or indeed of any such special capillary bearing region.

Scopelengys tristis Alcock

I have confirmed Alcock's (1899) finding that this species has no swimbladder.

Family SCOPELOSAURIDAE

In this family, which consists of several species belonging to a single genus, the swimbladder is absent in adolescent and adult individuals. The larvae have not been examined.

Suborder ALEPISAUROIDEA

Elsewhere I have stated that these iniomous fishes have no swimbladder (Marshall, 1955).

Order MIRIPINNATI

The swimbladders of these oceanic fishes have already been described (Bertelsen and Marshall, 1956). During the larval phase the swimbladder is functional, but it regresses during the adolescent phase and in *Mirapinna*, at least, is a rudimentary structure in the adult.

There are two retia mirabilia receiving blood-vessels that extend forwards from the posterior end of the swimbladder. In a larval *Parataeniophorus gulosus* of standard length 27.5 mm. the front part of the sac is thick-walled and the walls are invested with a well-developed gas-gland on either side. The posterior part of the sac is thin-walled and is presumably concerned in the resorption of gases.

In an adolescent *P. festivus* of standard length 42.0 mm. the thin-walled part of the swimbladder is much reduced and the retia mirabilia and gas-gland have begun to regress. In the rudimentary organ of *Mirapinna*, these structures are barely recognizable.

Order CETUNCULI

Family CETOMIMIDAE

Ditropichthys storeri (Goode & Bean)

St. 2059, 09° 11.4' S., 05° 17.4' W., 30. iv. 37, N 450 B, 1900-1400 m. Standard length 30 mm.

In this fish a small swimbladder was found with a strong attachment to the roof of the stomach. The sac measured about 2.5 mm. in length. Entering the posterior end of the sac was an artery coming from a vessel running along the stomach wall. Another vessel originating in the roof of the body-cavity ran to the 'anterior' end.

Transverse sections through this organ revealed it to be much regressed, the small lumen having a curiously complicated form. Much of the bulk of the swimbladder is formed by a voluminous submucosa. The sections suggest that during the regression of the organ, the sac becomes doubled back, the anterior and posterior ends coming together at the back. Within the lumen there were remnants of the cells composing the gas-gland.

The interpretation of this curiously regressed organ must be left until earlier stages in the life-history become available. Evidently the larvae of this species have a well-formed gas-filled swimbladder.

Cetostoma regani (Zugmayer)

No trace of a swimbladder was found in this species.

Family RONDELETIIDAE

Rondeletia bicolor Goode & Bean

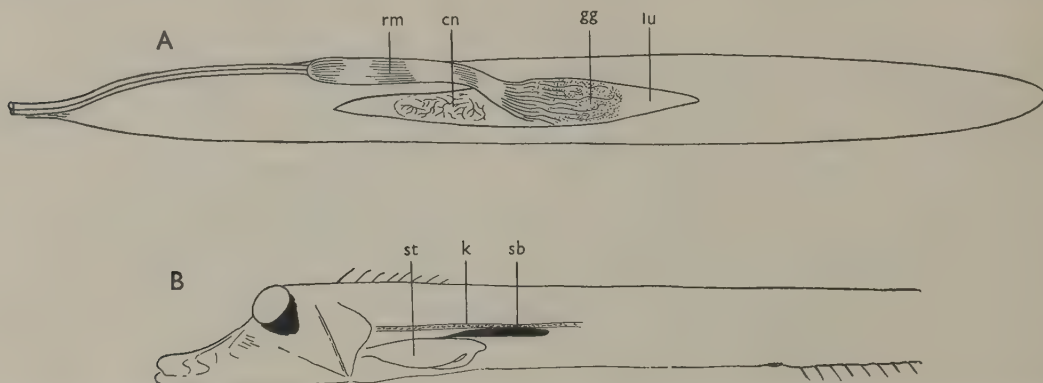
Parr (1929) records the absence of the swimbladder in this species.

Order GIGANTUROIDEA

Regan (1925) included the absence of a swimbladder in his diagnosis of this order. I was unable to find any trace of this organ in a *Gigantura vorax* of standard length 74 mm.

Order LYOMERI

Bertin (1934) has given an account of the internal organs of *Eurypharynx pelecانoides* and *Saccopharynx ampullaceus*, but no mention is made of a swimbladder. I was unable to find this organ in an individual of the first species.



Text-fig. 25. Swimbladder of *Stylophorus chordatus*, seen (A) from below, and (B) in the body-cavity of the fish. *cn*, capillary network; *gg*, gas-gland; *k*, kidney; *lu*, lumen of swimbladder; *rm*, rete mirabile; *sb*, swimbladder; *st*, stomach. (A, $\times 15$; B, $\times 1.8$.)

Order ALLOTRIOGNATHI

Family STYLOPHORIDAE

Stylophorus chordatus Shaw (Text-fig. 25)

St. 296, 8° 12' N., 18° 49' W., 26. viii. 27, TYF, 450-500(-0) m. Standard length 177 mm.

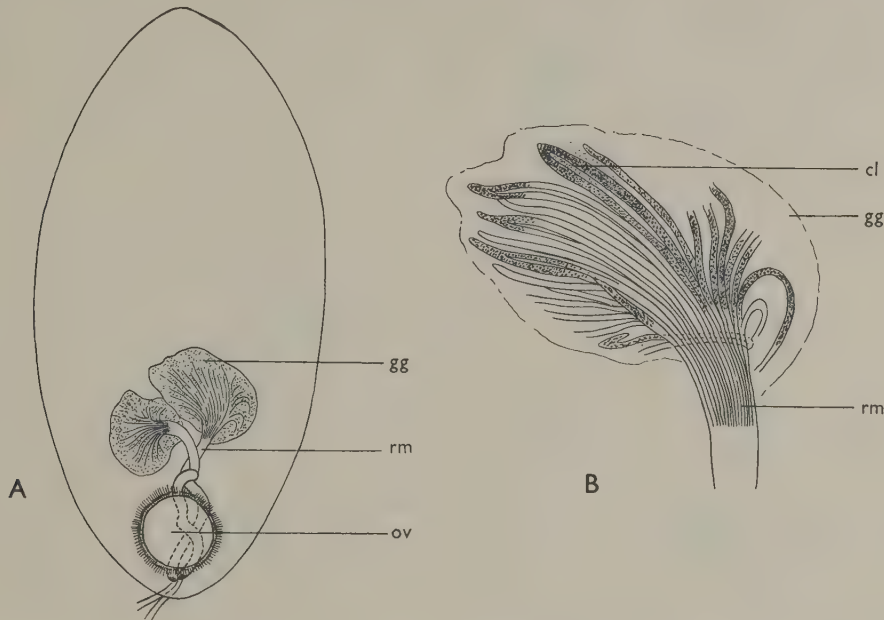
This individual contained a small elongated swimbladder, lying just below the black-speckled kidneys and originating a little before the pyloric end of the stomach. The sac measured about 12.5 mm. in length and 1.0 mm. in diameter and is attached by a mesentery to the dorsal wall of the stomach.

Within the mesentery is an artery and vein running close together to the anterior end of the sac. The two vessels continue together for about 3 mm. along the left-hand lateral walls and then subdivide to form a single rete mirabile having a length of about 2 mm. The rete enters the lumen of the sac about half-way along its length (of about 4 mm.).

Examination of serial transverse sections revealed the disposition of the resorbent and glandular parts of the swimbladder. The capillaries of the former lie just below the inner epithelium and occur over much of the lumen anterior to the point of entry of the rete. The glandular tissue lies behind this point in the posterior half of the lumen. In supplying the gland, the retial capillaries do not unite to form larger vessels. The rete is thus unipolar.

Reference to Text-fig. 25 will show the small volume of the lumen compared with the total volume of the sac. Between the inner epithelium and the tunica externa is a voluminous layer of lamellar fibres belonging to the submucosa, which thus makes up most of the total volume. Clearly this is a regressed swimbladder, which is doubtless relatively better developed during the early life-history.

In having a swimbladder with clearly separate glandular and resorbent parts, *Stylophorus* is evidently an euphysoclist. But it is unusual in having these two parts reversed in position, for in most euphysoclists (without an oval) the fore part is secretory, while the rear part is resorbent.



Text-fig. 26. Swimbladder of *Stephanoberyx monae*, seen (A) from above. In (B) is shown the blood supply to the right lobe of the gas-gland. *cl*, capillary loop; *gg*, gas-gland; *ov*, oval; *rm*, rete mirabile. (A, $\times 5.5$; B, $\times 17$.)

Order BERYCOMORPHI

Family STEPHANOBERYCIDAE

Stephanoberyx monae Gill (Text-fig. 26)

Oregon St. 1426 ($29^{\circ} 07' N.$, $87^{\circ} 54' W.$), 24. ix. 57, 600 fathoms, trawl. Standard length 83.5 mm. (16.0 $\times$ 8.0 mm.).

The swimbladder of this species is ellipsoidal in form and extends down most of the length of the upper part of the body-cavity.

The blood supply for the retia enters the floor of the sac close to its posterior end. The artery and vein form two long retia mirabilia (about 8 mm. in length). In the fish dissected the retia were displaced in position, but presumably extend forward along the swimbladder floor. Each rete runs to a corresponding lobe of the gas-gland, where the capillaries form loops running through the secretory tissue. The retia are thus unipolar in structure.

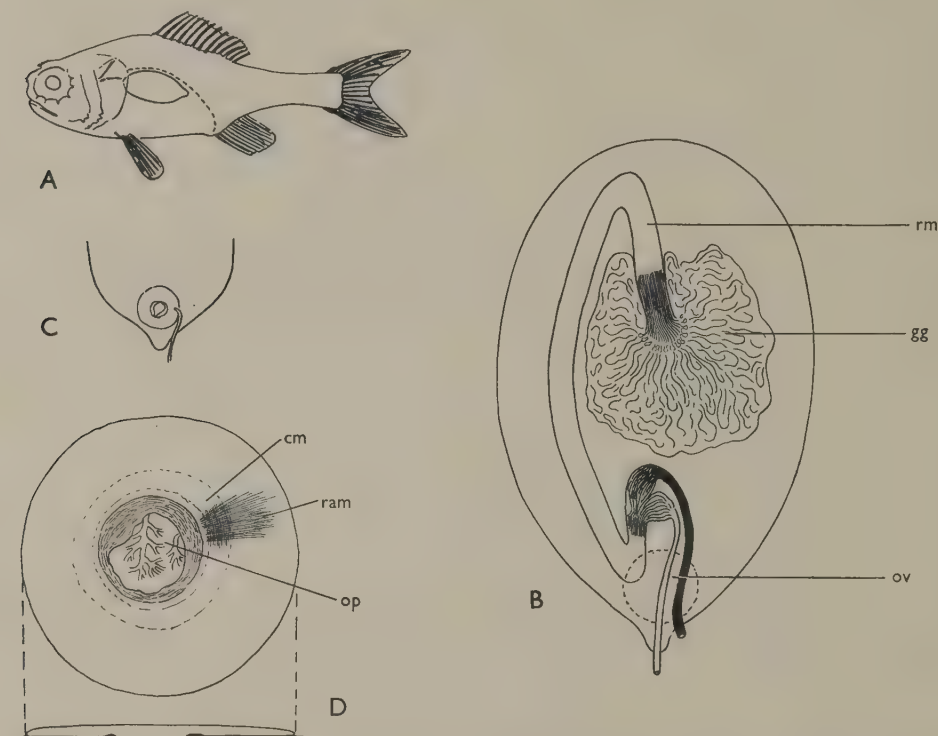
Immediately above this point of entry of the retial blood supply there is an oval on the roof of the sac. This measured about 5 mm. in diameter and was partly closed. The capillary network of this resorbent structure was plainly visible under the high power of a binocular microscope.

Family MELAMPHAIDAE

Melamphaes megalops Lütken (Text-fig. 27)

St. 13° 25' N., 18° 22' W., 28. x. 25, 4½-m. net, horizontal 900(-o) m. Standard length 56 mm. (8.5 × 5.0 mm.).

In this species there is a capacious swimbladder which, when fully inflated, must occupy about three-quarters of the length of the upper part of the body-cavity.



Text-fig. 27. Swimbladder of *Melamphaes megalops*, seen (A) in fish; (B) ventrally, and (c) dorsally (posterior end). The oval is shown in (D). *cm*, circular muscles of oval; *gg*, gas-gland; *op*, opening of oval into cavity of swimbladder; *ov*, oval; *ram*, radial muscles of oval; *rm*, rete mirabile. (A, × 1; B, × 10; C, × 5; D, × 25.)

At the posterior end of the sac, an artery and vein run forward to supply a single rete mirabile, which measures about 12 mm. in length. After its formation the rete runs backwards but soon bends sharply to run along the right-hand side of the gas-gland. Having reached a point ahead of the forward edge of the gas-gland, it turns back to enter the gland. Here it separates into capillary loops that meander among the secretory cells. As in *Stephanoberyx*, the rete is unipolar. An extensive gas-gland covers the median part of the swimbladder floor, the length and breadth being about 3 mm.

Just in front of the posterior tip and on the roof of the sac is an oval (about 2 mm. in diameter), which was almost closed, the entry into the sac measuring about 0.5 mm. in width.

The circular sphincter muscles that close the oval could be seen around the rim of the opening, where they are crossed by the long relaxed fibres of the radial complex. When these contract, the oval is expanded, the capillary network then being fully exposed to the gases in the swimbladder. During this phase gases are free to diffuse into the blood.

Melamphaes unicornis Gilbert (Text-fig. 28E, F)

St. 3484, 39° 55' N., 20° 01' W., 1. x. 56, IKMT, 750(-0) m. (estimated). Standard length 51 mm. (6.5 × 2.5 mm.).

The swimbladder of this melamphaid, which was quite relaxed, lies above the posterior half of the stomach.

Blood-vessels running down from the roof of the body-cavity enter the swimbladder roof at the posterior end, where they supply the oval, which was completely closed.

The single rete mirabile is about 3 mm. in total length. Since the sac is much contracted the rete may well have been displaced forward from its natural position. In this swimbladder it originates in a median lateral position and runs forward and across the floor of the sac, then turning backward to the gas-gland, which is indented along its posterior edge.

Melamphaes mizolepis (Günther) (Text-fig. 28B-D)

St. 288, 00° 56' S., 14° 08.5' W., 21. viii. 27, YFT, 250(-0) m. B.M. Reg. no. 1930.1.12. 1031-40. Standard lengths of two individuals examined 15 and 37 mm.

In the smaller of the two fishes dissected a small spherical swimbladder was discovered over the anterior part of the stomach. It measured 0.4 mm. in diameter. The rete mirabile runs forward to enter the posterior part of the swimbladder roof and then turns sharply downward to follow the outline of the organ as far as the front part, where it joins the gas-gland. This is a compact spherical structure almost filling the lumen.

The posterior tip of the rete appeared to be closely bound to the stomach. Actually two branches from the blood-vessels running over the stomach enter the rete.

The structure of the swimbladder in the larger fish was very similar. The diameter was 0.8 mm. In both individuals it is obvious that the swimbladder is little more than a regressed organ.

Melamphaes cristiceps Gilbert

St. 101, 33° 50' to 34° 13' S., 16° 04' to 15° 49' E., 15. x. 26, N 450 H, 1310-1410 m. B.M. Reg. no. 1930.1.12. 1006-8. Standard length of fish 80 mm.

A small swimbladder was found behind the stomach and just in front of the ovaries. It measured 3.5 mm. in length. As in *M. mizolepis*, the rete mirabile runs round much of the swimbladder before entering the gas-gland. It is evident that the swimbladder of this species is also regressed.

A fully developed swimbladder is also found in *Melamphaes macrocephalus*, *M. nigrofulvus*, *M. opisthopterus* ? *M. nycterinus* and *M. cristiceps* ? (Kanwisher and Ebeling, 1957).

Family ANOPILOGASTRIDAE

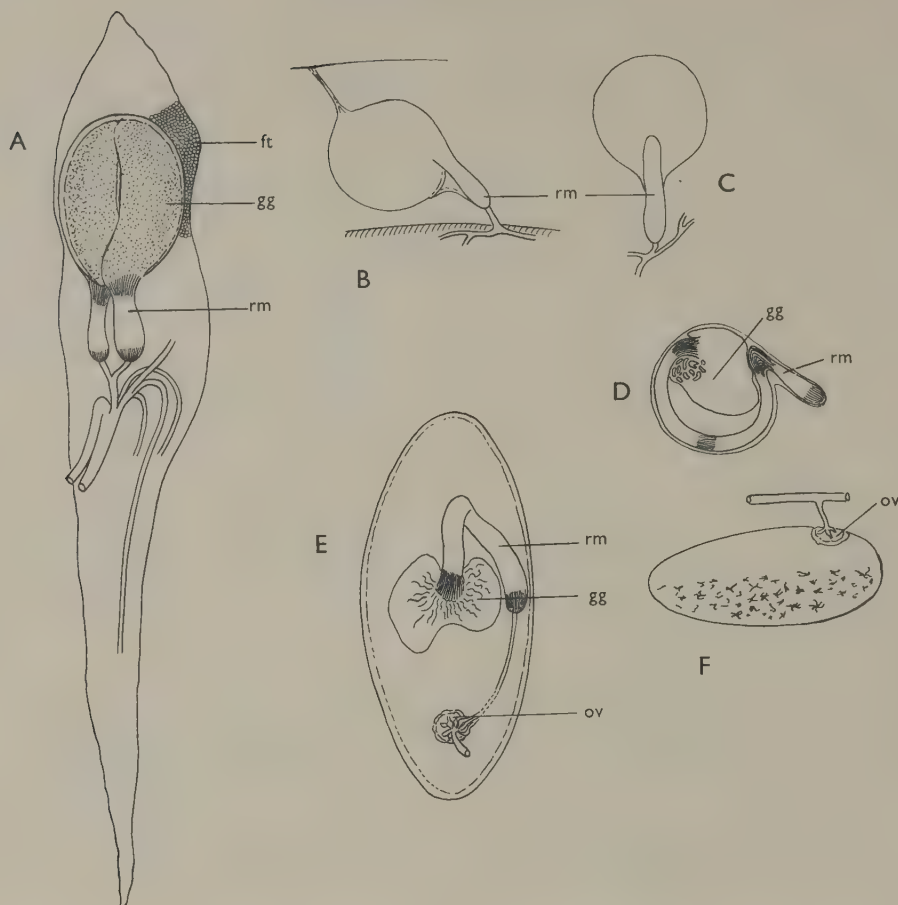
Anoplogaster longidens (Gill) (Text-fig. 28A)

St. 239, 46° 56' S., 46° 03' W., 2. vi. 27, N 450, 1050-1350(-0) m. B.M. Reg. no. 1930.1.12. 974-6. Standard length of fish 98 mm.

In the medium-sized individual examined the swimbladder was found to be a small, almost spherical sac overlying the foremost part of the stomach. Excluding the retia mirabilia, it measured rather more than 3 mm. in length and about 2 mm. in greatest depth. The walls are thick and tough.

Two retia mirabilia about 1 mm. in length enter the posterior end of the swimbladder, each running to a lobe of the gas-gland. Together the two glandular lobes invest the floor and lateral walls of the sac.

The swimbladder is surrounded by fatty tissue which is continued backwards for about 20 mm. to taper off above the end of the stomach. The blood supply for the retia mirabilia came from vessels within the fat body.



Text-fig. 28. Swimbladders of *Anoplogaster longidens* (A) seen from below; *Melamphaes mizolepis*, (B) lateral view, (C) dorsal view, (D) lateral view; *M. unicornis*, (E) dorsal view; (F) lateral view. *ft*, fat investment; *gg*, gas-gland; *ov*, oval; *rm*, rete mirabile. (A, $\times 8.5$; B, C, D, $\times 25$; E, $\times 10$; F, $\times 6$.)

From this dissection it would appear that in adult *Anoplogaster* the swimbladder can have very little hydrostatic function.

Order PERCOMORPHI

Family CHIASMODONTIDAE

Chiasmodon niger Johnson (Text-fig. 29)

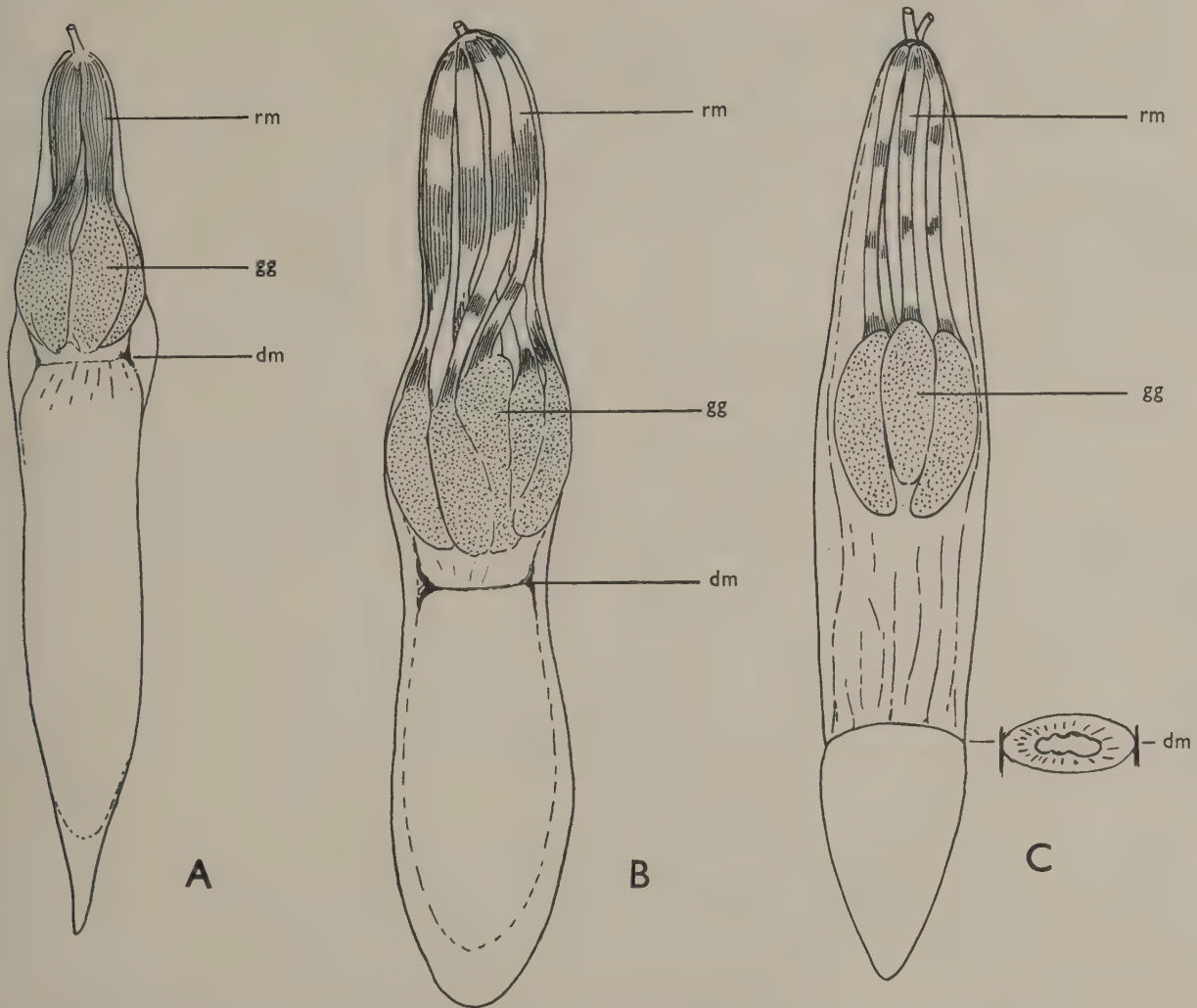
St. 239, $46^{\circ} 56' S.$, $46^{\circ} 03' W.$, 2. vi. 27, N 450 H, 1050–1350(–0) m. B.M. Reg. no. 1930.1.12. 1058. Standard length 50 mm. (8.0×1.5 mm.).

Position, $6^{\circ} 55' N.$, $15^{\circ} 54' W.$, 2-m. tow-net, horizontal, 800(–0) m. B.M. Reg. no. 1930.1.12. 1057. Standard length 49 mm. (8.0×1.5 mm.). B.M. Reg. no. 1922.5.26. 1–2. Madeira. Standard length 104 mm. (21.0×3.0 mm.).

In each of the three fishes examined, the swimbladder is an elongated ellipsoidal sac, which in the 104 mm. specimen occupied the greater part of the upper half of the body-cavity.

The retia are formed from an artery and vein that enter the forward tip of the sac. In the 49-mm. fish there were eight, each running backward to supply a corresponding lobe of the gas-gland and having a length of 3.25 mm. A closely similar retial measurement was also obtained from the largest individual.

In the 50-mm. fish a transverse diaphragm was found in the posterior half of the swimbladder. There is an aperture in the central part of the diaphragm, through which the anterior chamber containing the retia and gas-gland, communicates with the posterior chamber. It is clear that the structure of the swimbladder of *Chiasmodon* is essentially similar to that found in other physoclist teleosts, in which a diaphragm separates an anterior gas-producing chamber from a posterior resorbent



Text-fig. 29. Swimbladder of *Chiasmodon niger* (ventral view), seen in three different states of activity; (A) with the resorbent posterior chamber well expanded, (B) with the gas-secreting and resorbent chambers about equal in volume, and (C) with the gas-secreting chamber well expanded. *dm*, diaphragm; *gg*, gas-gland; *rm*, rete mirabile. (A, $\times 6.9$; B, $\times 19.5$; C, $\times 18$.)

chamber. It is also evident that the relative volumes of these two chambers vary in the three specimens. In the largest fish the diaphragm is close behind the gas-gland in the anterior third of the swimbladder, while it occupies a median position in the 49-mm. individual. These variations will be considered at greater length in the section concerned with gas resorption (p. 81).

The swimbladder is absent in two other members of the Chiasmodontidae, *Pseudoscopelus scriptus* and *Dysalotus alcocki*.

Order *PEDICULATI*

Suborder CERATIOIDEA

The combined researches of Garman (1899), Waterman (1948), R. Clarke (1950) and Bertelsen (1951) show that the deep-sea angler fishes have no swimbladder. Bertelsen's work reveals that this organ is also absent in the larvae.

STRUCTURE AND SYSTEMATICS

The foregoing survey has revealed that the species of major groups of bathypelagic fishes (Stomiatoidea, Salmonoidea, Myctophidae and Anoplogastroidea) have swimbladders conforming to an individual structural pattern or bauplan. Within each group there are, so to say, variations on an original structural theme. The bearing of these findings on classification will now be considered.

Order *Isospondyli*

Deep-sea isospondylous fishes with a swimbladder are all physoclists: they lack a pneumatic duct, which in physostomatous Isospondyli connects the swimbladder to the foregut. The acquisition of a closed swimbladder in these stomiatoids and deep-sea salmonoids must have been imposed on them by their living-space in oceanic mid-waters. The physostomatous isospondyls live in the relatively shallow seas over the continental shelves, or in freshwater. While at least some of these forms can secrete gas, this is a slow process, but they are readily able to inflate their swimbladders by gulping in air at the surface and forcing it down the pneumatic duct. On the other hand, a visit to the surface by a hypothetical physostome living several hundred metres below the surface is clearly 'out of the question'. Such a fish would not only be faced with a long climb to the surface, but having replenished the swimbladder gases, would then have to resolve the problem of the gradient in hydrostatic pressure as it returned to its level in the ocean. After diving to a depth of say, 500 m., the volume of the swimbladder would be compressed to about one-fiftieth of its capacity at the surface. If the fish is to use its swimbladder as a hydrostatic organ, it must then secrete gas, and to make up the volume (to 5 per cent of the body volume, see p. 68) at a pressure of 50 atmospheres would obviously require highly developed retia mirabilia and gas-glands. The retention of a pneumatic duct and air-gulping habits by a mid-water, deep-sea fish is therefore a biological *reductio ad absurdum*.

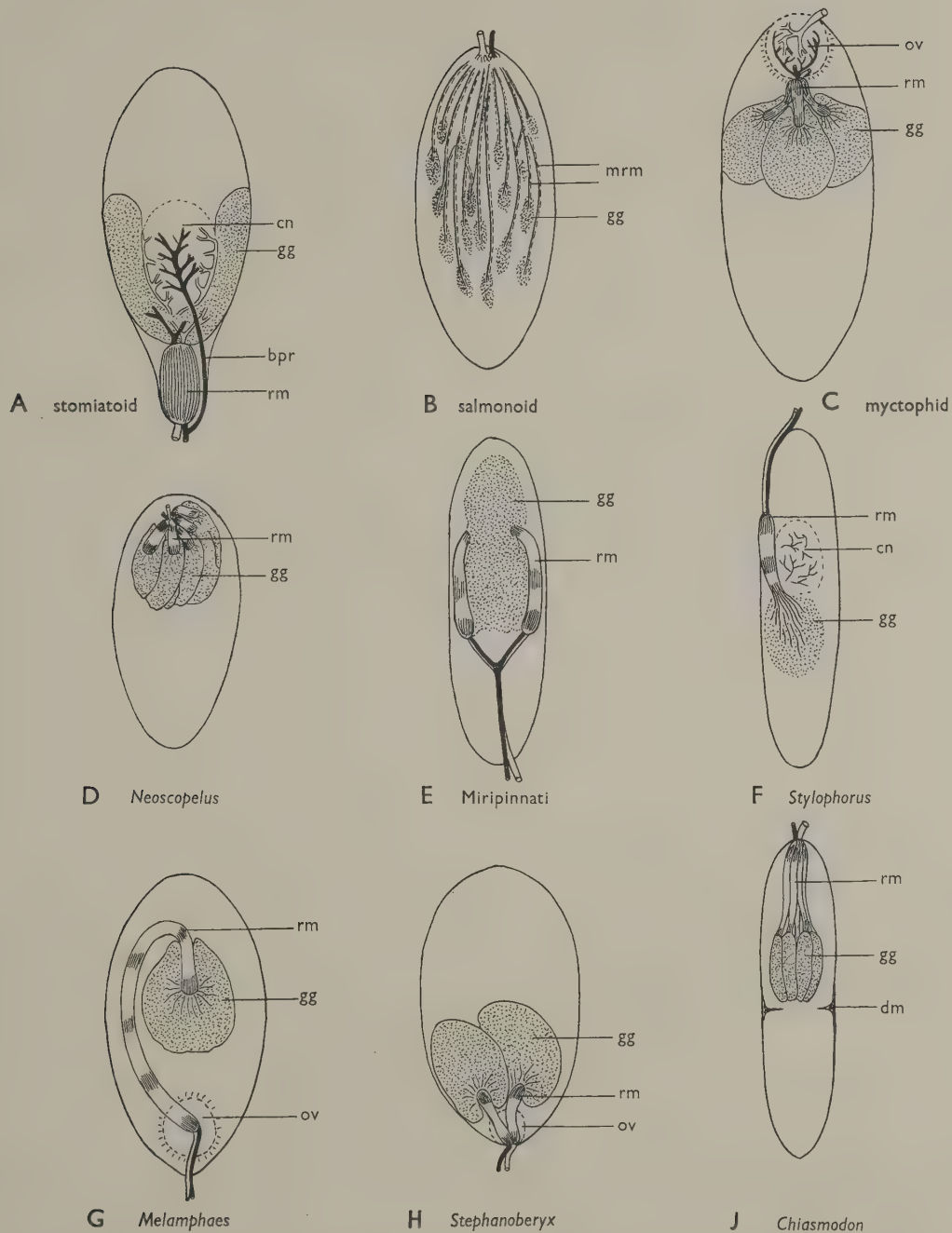
Suborder Stomiatoidea

The stomiatoid swimbladder has a character complex which may be defined as follows: It is paraphysoclistous¹ with a single, bipolar rete mirabile at the posterior end. As might be expected, the blood supply to the rete comes from vessels originating behind the swimbladder. The capillary network of the resorbent surface arises from a side branch of the retial artery and part of the venous circulation to the gas-gland. The venous blood thus eventually passes through the rete. The gas-producing complex is highly developed, the gland consisting of one to four lobes. A schematic diagram is shown in Text-fig. 30A.

Comparison of this definition with that of any of the following groups (pp. 53-56) will fully reveal the very characteristic design of the stomiatoid swimbladder. It will also provide further support for the classification of the stomiatoids as a distinct suborder of the Isospondyli.

Regan (1923) was the first to appreciate the essential unity of the stomiatoids. His definition of the

¹ This term was introduced by Rauther (1922) and refers to simple closed swimbladders in which the glandular and resorbent parts are not sharply localized. It is contrasted with the euphysoclistous type, the resorbent part of which is clearly separate from the glandular part, being either in the form of an oval, or an anterior or posterior section of the sac. In the latter forms, the two parts are often divided by a diaphragm. Fänge (1953) has also pointed out that in euphysoclists the resorbent part is thin-walled, while the glandular part is thick-walled. In paraphysoclists there is no such distinction.



Text-fig. 30. Schematic diagrams showing the essential structural features of the swimbladders of (A) stomiatoids, (B) deep-sea salmonoids, (C) Myctophidae, (D) *Neoscopelus*, (E) Miripinnati, (F) *Stylophorus*, (G) *Melamphaes*, (H) *Stephanoberyx*, (I) *Chiasmodon*. Arteries shown black, veins white. *bpr*, by-pass branch of retial artery; *cn*, resorbent capillary network; *dm*, diaphragm; *gg*, gas-gland; *mrm*, micro-rete mirabile; *ov*, oval, *rm*, rete mirabile.

group was later somewhat amplified (Regan and Trewavas, 1929). The stomiatoids were regarded as being most closely related to the clupeoids, but differing from them in possessing photophores. Certain alepocephalids and searsids, which are clupeoids, also have light organs, but the individual feature of the stomiatoid photophore pattern is the presence of one or two series of lights along each side of the mid-ventral line and one or more photophores associated with each eye (Brauer, 1908; Marshall, 1954).

It is evident that much of Regan's appreciation of the stomiatoids could not be put into words.¹ At all events his definition of them has proved to be inadequate. But when the swimbladder characters are considered together with those Regan used, the stomiatoids are revealed as a 'natural' monophyletic group. The implications of this will best be discussed at later stages in this systematic section.

Turning now to the arrangement of the stomiatoids into families, study of the swimbladder provides no new insight. It will be remembered that the Chauliodontidae, Melanostomiatidae, Malacosteidae and Idiacanthidae have no swimbladder, while such features as can be seen in the rudiments of this organ in certain of the Stomiatidae are merely typical of the suborder. Even in the Gonostomatidae, Sternoptychidae and Astronesthidae, which have swimbladders, the knowledge gained has little bearing on their relationships. This may best be shown by the following illustration:

Considering the first two families, Hubbs (1953) has cogently urged that they should again be referred to a single family, Sternoptychidae, with subfamilies Gonostomatinae, Maurolicinae and Sternoptychinae. Hubbs sees these subfamilies (in the order given) as forming a series ranging from forms with generalized to those with specialized body-shapes. Comparison of the swimbladder structure in the three groups also shows that there are no clear-cut differences between them, but if swimbladder characters alone were considered, the Astronesthidae could also be put with them (and into the same family). However, the other characters of the Astronesthidae indicate that they are best regarded as a separate family and that they are closer to the Chauliodontidae and Melanostomiatidae than to the gonostomatids and sternoptychids (Regan and Trewavas, 1929).

At the generic level, however, swimbladder characters can be of use in definitions, but not always. This may best be shown by short descriptions under the genera that were studied:

Family GONOSTOMATIDAE

Gonostoma. The differences between the swimbladders of *G. denudatum* and *G. elongatum* are so great that no common features can be found to typify the genus.

Cyclothone. The larval swimbladder (in which the gas-gland is found anteriorly), regresses and becomes invested with fat in the adult.

Pollichthys. An oval-shaped resorbent area on the floor of the swimbladder is surrounded by a horseshoe-shaped, single-lobed gas-gland. The bladder is ellipsoidal in form.

Vinciguerria. The resorbent area lies between the rete mirabile and a boomerang-shaped single-lobed gas-gland, which extends over the floor and side walls of the median part of the swimbladder.

Photichthys. The swimbladder of this gonostomatid is readily distinguished from those of other genera by its elongated tubular form.

Maurolicus. The gas-gland consists of two pairs of lobes, a smaller pair near the rete mirabile and a larger pair on the floor of the mid-region of the bladder. The resorbent area lies between these lobes.

Bonapartia. There is a single lobe to the gas-gland, immediately in front of which comes the resorbent area, which invests the floor of the swimbladder.

Ichthyococcus. The gas-gland has three lobes.

Family STERNOPTYCHIDAE

Sternoptyx. The gas-gland is three-lobed, while the resorbent area lies between and beyond these lobes.

¹ Pantin (1954) aptly calls such recognition 'aesthetic', as opposed to the analytical deductive methods that the systematist must eventually use.

Argyropelecus. The gas-gland surrounds the resorbent area which is on the floor of the swimbladder. The form of the swimbladder is ellipsoidal but approaches that of a sphere.

Polyipnus. The gas-gland is bilobed and the resorbent area lies between the lobes. In the adult the swimbladder is invested with fat.

It will be seen that certain swimbladder features, particularly the form of the gas-gland and its position relative to the resorbent area, can be used as diagnostic features in certain of the genera. Perhaps the associated circulatory system could also have been used; for instance, in the genera *Vinciguerria*, *Maurolicus* and *Pollichthys*. But the circulatory system can vary considerably within a genus and its species (see Godsil and Byer's (1944) study of the tunnies). Until more data are available it would seem best not to use the arrangement of blood-vessels as taxonomic characters.

Lastly, this survey has not been wide enough for much to be said on the distinguishing of species of deep-sea fishes by means of individual swimbladder structures. In one genus, *Gonostoma*, the three species are very unlike in this respect; I have already written (Marshall, 1950, 1954, 1955; Jones and Marshall, 1953) that *G. denudatum* has a normal type of swimbladder, that in *G. elongatum* the swimbladder regresses and becomes invested with fat, and that *G. bathyphilun* has no swimbladder. Differences of this order would seem, at first sight, to call for separate generic status for these three species. But reference to the papers just mentioned will show that there is a correlation between the degree of development of the swimbladder and the vertical distribution of each species. There seem to be parallel correlations in eye-structure, coloration (Marshall, 1954) and in other features (pp. 99-100). As closer study of such correlations is in progress, review of the status of the genus *Gonostoma* will be left until this work is completed. At present, however, there seems little justification for changing the present classification.

Suborder Salmonoidea

The design of the swimbladder in the deep-sea salmonoids is very unlike that of the stomiatoids. The individual features are as follows: The swimbladder is euphysoclistous¹ (see footnote on p. 50) and the blood-vessels forming the retial system break up into numerous micro-retia, each consisting of a relatively small number (less than 50) of arterial and venous capillaries (or arterioles and venules). The gas-gland is diffuse rather than compact (Text-fig. 30B).

The deep-sea salmonoids undoubtedly form a compact, natural group within the suborder Salmonoidea. Günther (1866) placed *Argentina* and *Microstoma* in the Salmonidae and Brauer (1906) regarded *Winteria* and *Opisthoproctus* as other members of this family. Trewavas's (1933) anatomical study of *Opisthoproctus* properly revealed its salmonoid affinities, while the later work of Chapman (1942a, b, 1943, 1948) clearly established the relationships between the above genera and *Rhynchogyalus*, *Bathylagus*, *Leuroglossus*, *Dolichopteryx* and *Macropinna*. More recently, Bertelsen (1958) has shown that *Xenophthalmichthys* is also an argentinoid fish, being closely related to *Microstoma* and *Nansenia*.

After Berg (1940) had introduced a new suborder (Opisthoproctoidei) for *Opisthoproctus*, Chapman (1942b) subscribed to this opinion, but proposed that all the other genera should also be included in the new suborder (Berg puts them in the Salmonoidea).

The swimbladder characters support Chapman's contention that *Opisthoproctus* should not be placed apart from the other deep-sea salmonoids. To Chapman's (1942a) list of characters for his 'opisthoproctoid' fishes may be added those given above concerning the swimbladder. Furthermore, the similarities in the design of the swimbladder are so striking that some support is given to Hubbs's

¹ In *Argentina*, *Glossanodon*, *Microstoma* and perhaps in *Nansenia* the posterior part of the swimbladder is thin-walled and functions as the resorptive part of the sac. In *Opisthoproctus* and *Winteria* this part of the sac may also have this function, but the material available was not sufficient to confirm this suspicion.

(1953) idea of putting the deep-sea salmonoids into a single family, Argentinidae. (At present they are grouped into the families Argentinidae, Bathylagidae, Microstomidae, Xenophthalmichthyidae, Dolichopterygidae, Winteriidae, Macropinnidae and Opisthoproctidae.) While Hubbs may be wanting to make too great a leap in the other direction, there would seem to be good reason for regrouping of these fishes to give better expression of their relationships. Perhaps the suborder Salmonoidea might be split into the divisions Salmoniformes and Argentiniformes, the latter containing the deep-sea forms. The last four families, in parentheses above, could be united into one, Opisthoproctidae, following Hubbs's first suggestion in his paper, while *Xenophthalmichthys*, in view of Bertelsen's (1958) work, could be included in the Microstomidae.

Order *Iniomi*

When defining this order, Berg (1940) wrote that the swimbladder, if present, has a pneumatic duct. The only iniomous fishes with a swimbladder are the Myctophidae and *Neoscopelus* (see also Marshall, 1955) and these have a closed swimbladder. There is nothing resembling a pneumatic duct in the adult, although the 'oval' in the myctophids may perhaps arise from the posterior part of the larval connection between the gut and the swimbladder. Like the stomiatoids, the iniomous fishes were most probably derived from an early type of teleost fish with an open swimbladder, and as Tracy (1911) suggested, the oval may have been evolved by a progressive reduction of the pneumatic duct. At all events, it would be interesting to study the development of the 'oval' in a myctophid.

The swimbladder of iniomous fishes is very unlike that of the stomiatoids and salmonoids. It is physoclistous¹ with three to five retia mirabilia which originate at the anterior end of the bladder. As might be expected, the retia draw their blood from vessels that arise in front of the swimbladder. Each rete usually supplies a corresponding lobe of the gas-gland.

Suborder Myctophoidea

The myctophid swimbladder is definitely euphysoclistous, having at the anterior end of the sac an 'oval' type of resorbent surface. There are always three unipolar retia mirabilia supplying the gas-gland (see Text-fig. 30c). These individual features provide more evidence for regarding the myctophids as a compact monophyletic group, but the ancestor of the myctophids can hardly have been 'derived from Isospondylous stock very like the Gonostomatidae' as Fraser-Brunner (1949) supposed. The differences between the stomiatoid and myctophid swimbladders are very considerable as Table 1 shows.

Table 1. *Stomiatoid and myctophid swimbladders*

	<i>Myctophidae</i>	<i>Stomiatoidae</i>
Swimbladder type	Euphysoclist (with oval)	Paraphysoclist
Number of retia	Three	One
Type of rete	Unipolar	Bipolar
Position of rete	Anterior	Posterior

In view of this, it is unlikely that the specialized swimbladder of a stomiatoid could have been transformed into that of a myctophid. As already suggested, the Myctophidae were probably derived from an early generalized form of isospondylous fish. The common origin of the myctophid and stomiatoid lines of evolution would thus be further back in the early history of the teleosts.

¹ I was unable to determine whether *Neoscopelus* was a euphysoclist or paraphysoclist.

Neoscopelus

Apart from the uncertainty of its type of swimbladder, this genus is readily distinguished from all myctophids in the number of retia mirabilia, there being more than three retia (five in two individuals that were examined (Text-fig. 30D). *Neoscopelus* has been classified within the Myctophidae, either as one of the genera, or as the type, of the subfamily Neoscopelinae (Fraser-Brunner, 1949). In many ways it is quite unlike the myctophids (*sensu stricto*), particularly in the arrangement and structure of the light organs (Brauer, 1908). Such differences, together with those found in the swimbladder, certainly indicate that the genus should be placed apart from the myctophids. As already suggested (Marshall, 1955), it might be better to put it into a separate family (Neoscopelidae) together with the genera *Scopelengys* and *Solivomer*.

Order Miripinnati

The basic features of the swimbladder of these fishes have already been described (Bertelsen and Marshall, 1956). In the sharp separation of an anterior thick-walled secreting part from a posterior thin-walled resorbent part, the organ is euphysoclistous, but there appears to be no diaphragm. The gas-gland receives its blood supply through two unipolar retia mirabilia that originate in the middle region of the sac and are formed from a posterior artery and vein (Text-fig. 30E).

The only known oceanic fishes with two such retia mirabilia are *Anoplogaster* and *Stephanoberyx*, but in the latter genus, and in the Melamphaidae, the resorbent part of the swimbladder is formed by an oval.

Order Allotriognathi, Family STYLOPHORIDAE

The swimbladder of *Stylophorus* is readily distinguished from those of other pelagic, deep-sea fishes. It is euphysoclistous with a single unipolar rete mirabile receiving blood from an artery-vein pair that originates in front of the forward end of the sac. Unlike most euphysoclists, the front half of the swimbladder is provided with a resorbent capillary system, while the rear half contains the gas-producing glandular tissue (Text-fig. 30F). The organ regresses during adult life.

Order Berycomorphi

The bathypelagic members of this group are mainly to be found in Regan's (1911) order Xenoberyces. The families are Stephanoberycidae,¹ Anoplogastridae and Melamphaidae. Parr (1929) also placed the Rondeletiidae in Regan's order, but Harry (1952) has provided ample evidence for regarding this family, together with the Barbourisiidae and Cetomimidae, as forming a 'natural group widely distinct from all other families of fishes...'. The three genera considered in this report, *Stephanoberyx*, *Anoplogaster* and *Melamphaes*, all have a closed swimbladder² with one or two unipolar retia mirabilia that originate at the posterior end of the sac.³ In *Stephanoberyx* and *Melamphaes*, the swimbladder is definitely euphysoclistous, for an 'oval' is present (Text-fig. 30G, H).

Regan (1911) decided that the Stephanoberycidae and Melamphaidae were sufficiently different from 'typical Berycomorphi' to be placed in a separate order, Xenoberces. They are also distinct in swimbladder characters. As we have seen, in *Stephanoberyx*, *Anoplogaster* and *Melamphaes*, there are one or two retia that originate at the posterior end of the swimbladder. In the Berycomorphi, as restricted by Regan, all available evidence shows that the retia originate at the anterior end of the sac (Rauther, 1922; Nelson, 1955).

¹ *Stephanoberyx* may be demersal rather than pelagic in habit.

² *Stephanoberyx* is said to have a pneumatic duct (Regan, 1911; Berg, 1940), but I was unable to find one.

³ Dr A. Ebeling, who is revising the Melamphaidae, has been good enough to tell me that in certain melamphids (*Melamphaes* s.s.) the retia are at the front of the swimbladder.

But such differences, together with those found by Regan, would hardly seem to require separate ordinal status. Regan himself felt that the Xenoberyces were 'probably derived from the same stock as the Berycomorphous fishes'. It would thus be preferable to regard the 'Xenoberyces' as a suborder of the Berycomorphi. The other fishes of this order (Regan's Berycomorphi) would form the other suborder.

The order Berycomorphi (*sensu lato*) may be defined as physoclistous teleosts with the anterior rays of the vertical fins spinous and with nineteen principal rays (seventeen of which are branched) in the caudal fin (eighteen principal rays with sixteen branched in the Polymixiidae). Pelvic fins subabdominal or thoracic, with or without a spine, and with three to thirteen soft rays. Mouth bordered above by protractile premaxillae; one or two supramaxillae. Orbitosphenoid present or absent.

Suborder Berycoidea: Families POLYMIIXIIDAE, BERYCIDAE, DIRETMIDAE, TRACHICHTHYIDAE, MONOCENTRIDAE, ANOMALOPIDAE, HOLOCENTRIDAE

Orbitosphenoid present; a subocular shelf usually developed, palate usually toothed one or two supramaxillae (Regan, 1911). Swimbladder with retia mirabilia originating at the anterior end of the sac.

Suborder Anoplogastroidea: Families STEPHANOBERYCIDAE, MELAMPHAIDAE, ANOPILOGASTRIDAE¹

No orbitosphenoid; no subocular shelf; palate toothless; a single supramaxilla, triangular in shape (Regan, 1911). Swimbladder with one or two retia mirabilia, usually posterior in position: an oval at the posterior end of the sac.

Order *Percomorphi*, Family CHIASMODONTIDAE

Like many other percomorph fishes, *Chiasmodon niger* has a euphysoclistous swimbladder with a diaphragm separating an anterior gas-producing chamber from a posterior resorptive chamber (Text-fig. 30J). Jones and Marshall (1953) and Fänge (1953) have drawn attention to percomorphs with this type of swimbladder.

To conclude, there is the problem of what the structural pattern of the swimbladder may add to present conceptions of the relationships between the major groups of deep-sea teleosts.

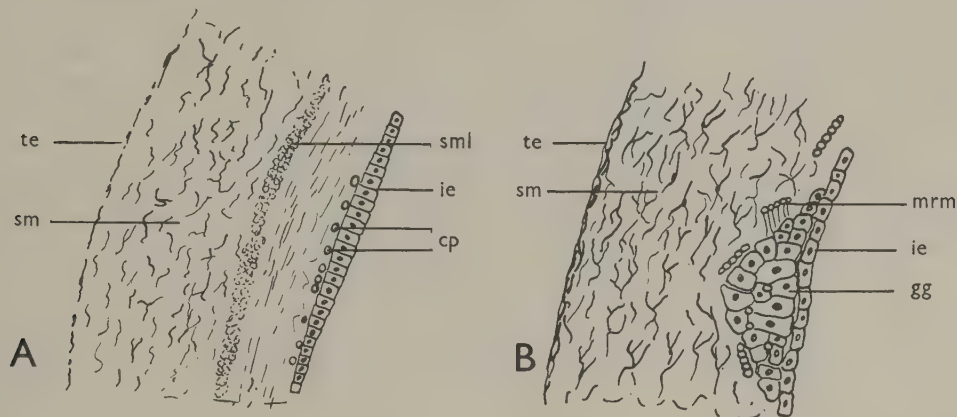
The Isospondyli undoubtedly contain the most generalized forms of teleosts. Although the fishes of each isospondylous suborder are specialized in varying degrees, they still retain certain characters of the early primitive teleosts. While the stomiatoids have special features, such as light organs, that are correlated with a bathypelagic mode of life, Regan (1923) looked on them as being quite similar to the clupeoids. He found the skull of *Photichthys* to be very like *Elops*, which is perhaps the most primitive of all living teleost genera. The extreme development of the gas-producing tissues of the swimbladder (or the complete loss of this organ) is also an adaptation to a deep-sea existence, but the structural pattern is quite unlike that in any other group, whether deep-sea or otherwise.

It is unlikely, as already stated, that the Myctophidae, with a very different form of swimbladder, were derived from a stomiatoid stock. In acquiring an oval, the myctophids have a remarkably advanced type of swimbladder relative to their position in the evolutionary scale of teleosts. Above the Iniomi, an oval is not encountered until the Anacanthini (cod-like fishes) are reached. However, an oval would seem to be no more efficient a resorbent surface than the capillary system in stomiatoids. *Astronesthes* is no more limited in its vertical migrations than the myctophids on which it feeds (see p. 88). From the functional as well as the structural aspect, the conclusion repeated in the first sentence of this paragraph seems to be justified.

¹ Grey (1955) has confirmed that *Anoplogaster cornuta* (Val) is the young of *Caulolepis longidens* Gill and also synonymizes the latter under the former (in accordance with the principle of priority in the International Rules of Zoological Nomenclature).

The Miripinnati and most Anoplogastroidea resemble the stomiatoids in having retia that are formed at the posterior end of the swimbladder, although both groups consist of euphysoclists, while all stomiatoids are paraphysoclists. The transformation of a stomiatoid type of swimbladder, with its unique vascular arrangements for the resorption of gases, to either the miripinnatous or anoplogastrid form would seem most unlikely. It is thus evident that the stomiatoids are a well-defined phyletic line of isospondylous fishes which, as the result of evolution in other directions, have left no living descendants.

Earlier discussion suggests this is also true of the deep-sea salmonoids. They are a compact, specialized group, forming a morphological (perhaps also an evolutionary) series towards forms like *Opisthoproctus*. However, the 'bauplan' of their swimbladder could very well have been derived from the more generalized condition seen in the salmonids.¹



Text-fig. 31. Semidiagrammatic representations of transverse sections through the swimbladder wall of (A) *Salmo*; (B) *Opisthoproctus*. cp, capillaries; ie, inner epithelium; gg, gas-gland; mrm, micro-rete mirabile; sm, submucosa; sml, layer of smooth muscle; te, tunica externa.

In *Salmo* the swimbladder is supplied with arterial blood through branches of the coeliaco-mesenteric and intercostal vessels. Venous blood leaves through a vessel running forward to the portal system and through others leading to the intercostal and gonadal veins. The capillary stem may here and there form associations, but there is no regular development of retia mirabilia. The inner epithelium over the forward part of the sac, consists of columnar cells, elsewhere of flattened or cubical cells (Rauther, 1922). All that is required to turn such a swimbladder into the deep-sea salmonoid type is the regular association of capillaries to form micro-retia mirabilia, the differentiation of the inner epithelium to form gas-glands and, of course, the loss of the pneumatic duct. This may be better followed in Text-fig. 31, which shows semi-diagrammatic, transverse sections through the swimbladder walls of *Salmo fario* and *Opisthoproctus soleatus*.

The lineages represented by the orders Iniomi, Cetunculi, Chondrobrachii and Miripinnati may well have evolved from a common ancestor. Presumably this ancestral fish had advanced beyond the level of organization of the primitive Isospondyli (in that its premaxillae excluded the maxillae from the biting edge of the upper jaw and the mesocoracoid arch was lost from the shoulder girdle). The orders Giganturoidea and Lyomeri may also belong to this evolutionary complex (Bertelsen and Marshall, 1956).

The only fishes in these orders with swimbladders are the Myctophidae, Neoscopelidae (Iniomi), and the Miripinnati. The Myctophidae and *Neoscopelus* are considered to be rather closely related,

¹ Fahlen (1959) has shown that there are (micro)-retia mirabilia in the swimbladder of *Coregonus lavaretus*.

and this, as we have seen, is supported by the similarities between their swimbladders. But there is little resemblance, other than that implied by the general label 'euphysoclist', between the miripinnatus and myctophoid type of swimbladder. Again, it would seem that the two groups are not closely related and that each is the result of a distinct evolutionary trend within the iniomous complex. But morphological knowledge of the various groups is by no means comprehensive. In time it may be possible to regard the Chondrobrachii, Cetunculi, Miripinnati and perhaps the Giganturoidea and Lyomeri as suborders of the Iniomi. At present their differences are more apparent than their similarities.

Whereas the Isospondyli are the basal group of soft-rayed fishes, the Berycomorphi occupy a similar position within the spiny-finned groups. These fishes have 'advanced' beyond the iniomous level of organization in the development of spinous rays in the vertical and pelvic fins. But like many of the soft-rayed fishes with a fully developed caudal fin, nearly all Berycomorphi have nineteen principal rays in this fin.

After their origin, the berycomorphs seem to have split up into two series of lineages, now represented by the suborders Berycoidea and Anoplogastroidea. The former group mainly consists of shallow and deep water fish, whereas in the latter the fishes are predominantly bathypelagic in habit. It is curious that like the stomiatoids among the Isospondyli, the purely deep-water group of berycomorphs acquired a swimbladder with a reversed polarity, the gas-secreting complex coming to a focus, as it were, at the posterior end of the sac. The differences between the stomiatoid and anoplogastroid swimbladder, to which some reference has already been made, are summarized in Table 2:

Table 2. *Swimbladder structure: Berycomorphi and Isospondyli*

<i>Swimbladder</i>	<i>Isospondyli</i> <i>Stomiatioidea</i>	<i>Berycomorphi</i> <i>Anoplogastroidea</i>
Type	Paraphysoclist	Euphysoclist (with oval)
Type of rete	Bipolar	Unipolar
Position of rete	Posterior	Posterior
Number of retia	One	One or two

As in the earlier comparison between the stomiatoids and myctophids, there is little reason to suppose that the second group might have been derived from the first. However, the berycomorphs may well have come from a primitive type of iniomous fish (in that its premaxillae alone formed the biting part of the upper jaw). The present-day representatives are all marine fishes and their evolutionary radiations, with the notable exception of the Holocentridae, have been mostly directed towards the deep ocean. Considering only marine teleosts, it looks as though some of the groups, that evolved during the early 'explosive' radiations of the soft-rayed and spiny-rayed teleosts, were 'edged out' from the more productive shelf-waters into the deeper, less favourable waters of the ocean.

As the common ancestor of both assemblages is likely to have had an open swimbladder, and as a closed one seems to be essential for an oceanic fish, it may well be that the physoclistous condition was independently evolved in the deep-sea Isospondyli and Berycomorphi. Furthermore, the same is probably true within the Isospondyli themselves, for it seems clear that the deep-sea salmonoids were derived from physostomatous stock (p. 55) and it is also evident that the stomiatoids were not part of this evolutionary line (p. 50). Again, the type of closed swimbladder possessed by the Myctophidae could well have been independently acquired. While the common ancestor of the soft-rayed and spiny-rayed groups must be sought at an early stage in teleost evolutionary history, the common factor in these developments of a closed swimbladder seems to be no more than residence in a living space in the deeper reaches of the ocean.

THE LARVAL SWIMBLADDER

The teleost swimbladder arises early in development as an outgrowth of the dorsal or lateral walls of the foregut. While the embryonic formation of the swimbladder in a deep-sea fish has yet to be described, the sequence of events is likely to be very similar to that in shallow water fishes. When considering the general features of myctophid larvae, Holt and Byrne (1911) mentioned that from a very early stage the roof of the swimbladder appeared to be darkly pigmented. It is also clear from Jespersen and Tåning's (1926) figures that the early post-larvae of gonostomatid fishes have a well-formed swimbladder. In post-larval *Vinciguerria* and *Maurolicus* I found the swimbladder to be full of gas.

The presence of gas in the larval swimbladder raises an interesting question concerning the early functioning of the organ in the deep-sea environment. In many shallow water fishes the sac is first inflated by the larvae gulping in air at the surface and passing it down the larval pneumatic duct (which disappears during later development in physoclists). While the larval life of most bathypelagic fishes is passed in the surface-layers, it seems likely that the eggs are shed at deeper levels. Hatching may thus take place as the eggs float upwards from the depths. If so, many larvae could be far from the surface-film when the larval swimbladder is ready to be filled with gas.

However, McEwan (1940) found that, in *Hemichromis*, the connection between the larval swimbladder and the gut never developed a lumen and, to make sure of the implications of this discovery, the early larvae were denied experimentally all access to the surface. In spite of this the larval swimbladder became filled with gas. McEwan found that at one stage the lumen was obliterated by the swelling of highly vacuolated cells forming the inner epithelium. Having expanded to the limit, these cells suddenly collapsed to form a flat epithelium, after which gas appeared in the cavity. If such a mechanism is found in deep-sea fishes, it is obvious that the larvae need not seek the surface-film in order to initiate the use of the swimbladder as a hydrostatic organ.

At least five species of *Cyclothone* (*braueri*, *signata*, *microdon*, *pygmaea*, and *acclinidens*) must have a gas-filled swimbladder during their larval life, but after metamorphosis the organ regresses and becomes invested with fatty tissue. Presumably this is also true for other deep-water fishes with a fat-invested swimbladder in the adult phase. All such species will best be considered in a separate section (pp. 65-68). In the Miripinnati (Bertelsen and Marshall, 1956) and *Stylophorus*, the larval swimbladder also undergoes regression, but does not serve as an attachment for fat in the adult.

Lastly, all available evidence shows that bathypelagic fishes, without any trace of a swimbladder when adult, are also without a definite larval organ. (I have examined larval paralepidids, scopelarchids, and melanostomiids without finding a swimbladder.) Furthermore, Bertelsen (1951) remarked that larval ceratioids, like the adults, have no swimbladder, but he suggested that 'gelatinous tissue under the skin, which is present in all Ceratioid larvae in more or less well-developed condition, could be regarded as a floating organ'. More recently, Shelbourne (1956) has seen a correlation between the pelagic habit in fish eggs and larvae and the development of large subdermal spaces in the young stages. As these spaces seem to be filled with low density fluids derived from the yolk, they act as buoyancy chambers. It is clear from Shelbourne's figures that voluminous subdermal spaces are developed regardless of the presence or absence of a swimbladder in the larval phase. This is also true of bathypelagic fishes. Larval myctophids belonging to species with a well-formed adult swimbladder (e.g. *Benthosema glaciale*, *Hygophum benoiti*, *Myctophum punctatum*) have large subdermal spaces, particularly in the head region (see Tåning's (1918) figures). Regarding fishes without a swimbladder, we have already referred to Bertelsen's findings in the ceratioids. It would

seem that the larval swimbladder is not sufficient to bring the specific gravity of the larva to that of the environment. 'Buoyancy tanks' are required as well.¹

THE SWIMBLADDER WALL

Excluding the peritoneal investment, there are four main layers of tissue in the swimbladder wall: an outer, closely-knit fibrous layer; a middle, loosely-woven, fibrous tissue layer; a layer of smooth muscle fibres, and an inner epithelial layer. The outer layer is usually known as the tunica externa, while Fänge (1953) called the middle layer the submucosa, for in structure and position it is very like the layer of the vertebrate gut that already has this name. As Fänge (1953) has said, '...from an embryological and comparative anatomical point of view the teleostean swimbladder is nothing else than an isolated part of the digestive tube, although adapted to special functions'. The inner layer consists of pavement epithelium, which is locally differentiated to form the gas-gland.

The swimbladder lies outside the coelom, between the gut and the kidneys. It is retroperitoneal in position, but it becomes invested in varying degrees with peritoneal tissue. While the dorsal edge of the peritoneum usually runs along the lateral walls of the swimbladder, in some teleosts this limit lies above the organ (Freunde, 1938). Between the peritoneum and tunica externa, there may be a padding of loose, reticular, connective-tissue cells. Strands of connective tissue also run between the roof of the sac and the outer coat of the kidneys, which lies close to the swimbladder wall.

The peritoneal coat and the tunica externa are mainly formed of closely packed collagen fibres. The submucosa is by far the most voluminous coating of the swimbladder wall and it usually consists of a reticulum of loosely packed, collagen fibres within a gelatinous ground-substance (Saupe, 1939; Fänge, 1953). This layer is particularly thick under the gas-producing structures of the swimbladder. Between the submucosa and the inner epithelium there is a layer of smooth muscle cells which I have been able to identify in a number of the fishes considered in this report.

From this general outline we may turn to closer consideration of the swimbladder wall in certain deep-sea teleosts.

Family STERNOPTYCHIDAE, *Sternoptyx diaphana*

The fine structure of the swimbladder wall of this hatchet fish has been described by Nusbaum-Hilarowicz (1920), who divided the layers of tissue into three sections: outer, middle and inner. The outer section consists of two layers of long connective tissue fibres, the fibrillar axes of the topcoat being at right angles to those of the undercoat. From his plate VIII, fig. 9 it is evident that the fibres of the undercoat describe circular paths about the long axis of the sac. The middle section is a loosely-woven reticulum of fibres, which are delicately fashioned and form most of the wall-thickness. The cavities between the fibres hold a homogeneous and transparent substance, which is not stained by such dyes as haematoxylin or eosin. Nusbaum-Hilarowicz suggested that in the living animal this substance is probably a serous fluid. Undoubtedly this layer corresponds to what Fänge (1953) called the submucosa, and he remarked that, '...the submucosa often has a jelly-like, half-fluid consistency'. As is usual, the inner layer consists of flattened epithelial cells which are locally differentiated to form the gas-gland.

Argyropelecus

The histology of the swimbladder wall of *Argyropelecus hemigymnus* was also described by Nusbaum-Hilarowicz. There is an outer layer, presumably the tunica externa, consisting of long fibres with elongated nuclei, which for the most part are set across the long axis of the sac. Underlying this

¹ It would be interesting to know whether pelagic fish larvae with a swimbladder have relatively smaller subdermal spaces than those without this organ.

circular layer is a thick layer (the submucosa) of fibres forming a loosely-woven reticulum. As in *Sternoptyx*, this fibre complex would appear to be developed within a gelatinous matrix. Last comes the inner, filmy coat of pavement epithelium.

Longitudinal sections were prepared of the specimen of *Argyropelecus olfersii* described on p. 20. The tissue composition of the walls is much like that of *A. hemigymnus*. Above the gas-gland, the roof has a thickness of 50–100 μ , most of this consisting of the submucosa. The floor of the sac under the gas-gland is about three times as thick as the roof, but this swimbladder was in a very relaxed state. When the swimbladder is taut and in the steady state, the walls must be a good deal thinner, even remembering that the above measurements have been taken from tissues shrunk by preservation and subsequent preparation.

Family GONOSTOMATIDAE, *Vinciguerria attenuata*

The swimbladder taken for sectioning came from a fish of standard length 32.5 mm. The sac was well expanded, the major and minor axes measuring 7.5 and 2.5 mm. The gas-gland was flattened and well displayed, appearing much like that of the fish described on pp. 7–9.

Over the roof of the rear part of the swimbladder the walls measured about 20 μ in thickness. There is a thin tunica externa formed of fibres running round the sac; then comes the reticulate submucosa which takes up most of the wall thickness. Near the rete mirabile the walls are padded with a voluminous submucosa measuring about 250 μ in thickness. The swimbladder is lined with a filmy pavement epithelium.

Vinciguerria nimbaria

The swimbladder described on p. 9 was used in the preparation of serial transverse sections. It is of particular interest in that the sac was much contracted, but not collapsed, while the gas-gland formed a thick bunched-up mass.

The swimbladder is completely invested by a layer of peritoneum bearing many melanophores and formed of close-set fibres. The thin tunica externa is made up of circular fibres, while the very thick submucosa varies from 50 to 100 μ in width. Owing to the relaxation of the sac, the fibres of the submucosa have been thrown into a series of undulations (see also p. 65).

Cyclothone

During the larval phase, the species of *Cyclothone* have a gas-filled swimbladder, which regresses and becomes invested with fat after metamorphosis to the adult. The development of the latter condition is dealt with in another section (pp. 65–68). Here we deal with the wall structure of the larval swimbladder.

The species of *Cyclothone* studied by Nusbaum-Hilarowicz (1920) was probably *braueri* and not *signata* (see p. 18). It is evident from his plate VIII that the swimbladder was in the larval condition, although fig. 3 shows a trace of the regular reticulate tissue (which holds the fat) at one end of the sac.

He found a thin but tough outer layer (tunica externa), consisting of long fibres that encircle the sac followed by another thin layer of rounded and branching cells. The next and median layer (submucosa) was very voluminous at the front and rear sections, but quite thin in the middle region. This was formed of fibrillar and loosely compacted tissue. The inner epithelial layer formed the gas-gland at the front of the sac.

Transverse sections through the swimbladder of a *Cyclothone braueri* of standard length 26.5 mm. revealed much the same tissue structure. The swimbladder has a length of about 3 mm. and around the gas-gland the walls have a thickness of from 100 to 200 μ .

A 10-mm. larval stage of *C. pygmaea* from Thor station 144 was also sectioned. There is little that need be added, except to mention that the sac is completely invested with a densely pigmented

peritoneal coat. This is formed of strong close-set fibres that tend to run along the major axis of the swimbladder.

Astronesthes niger

The swimbladder described on p. 23 was examined under a high-power binocular, the tissue layers of the walls being teased apart. The sac is completely enveloped by the peritoneal coat, which is constructed of close-set fibres that are set along the major axis. The underlying tunica externa is formed of circularly disposed fibres. Next follows the thick submucosa with its loose network of fibres that run in all directions.

Family MYCTOPHIDAE, *Myctophum punctatum*

A swimbladder measuring about 12 mm. in length and 5 mm. in depth was sectioned.

The peritoneum extends round the floor and lateral walls of the sac. It is formed of lamellar collagen fibres (about $5-10\mu$ in width) which run along the major axis of the sac. This layer carries melanophores. The underlying tunica externa is barely detectable, but is comprised of fibres that run round the swimbladder. As is usual, the submucosa forms most of the wall thickness, this being about 300μ under the gas-gland and about 50μ in the roof of the sac. Remains of the ground substance could be seen adhering to the loose fibrillar network. Here and there the cells of the ground substance could be detected. Finally, there is a filmy coat of pavement epithelium lining the inner surface of the sac.

Diaphus rafinesquei

Certain details of the structure of the swimbladder wall have been described by Rauther (1922). As in *Myctophum punctatum*, the fibrous peritoneum ('fibrose hülle') does not completely invest the sac but extends rather more than half way up the lateral walls. Between the peritoneum and what Rauther drew as a thick circular layer of fibres is a padding of loose, reticular connective tissue. The circular layer must represent the tunica externa and the submucosa. Microscopic examination of the swimbladder of the fish from Discovery station 3484 (see pp. 30-32) revealed other structural details.

At least at the forepart of the organ, the peritoneal coat extends over the roof of the sac. It is formed of fine and close-set collagen fibres together with a number of elastic fibres. The tunica externa consists of relatively strong fibres running round the sac, while the more delicate fibres of the submucosa form a loose network. As far as could be judged the lateral walls are about 50μ in thickness, the submucosa accounting for about nine-tenths of this dimension.

To summarize, the wall of the swimbladder usually has this structure: a voluminous loosely-woven reticulum of collagen fibres in a gelatinous ground-substance separates the thin, but tough outer fibrous layer from the inner, filmy epithelium lining the sac walls. Clearly this tissue-complex must have adequate mechanical, as well as gas-proofing qualities.

In the steady state any loss of gas by diffusion out of the sac can be countered by the activity of the gas-gland. Presumably the walls will be under tension without undue strain. It would also seem likely that the fibres of the submucosa will lie close together within the gelatinous matrix, so forming a densely matted tissue, not the loose reticulum seen in prepared sections.

Concerning the gas-proofing qualities, a fish living at a depth of 500 m. will most probably have 80 per cent of oxygen in its swimbladder gases, so the swimbladder wall must contain a pressure of 40 atmospheres of oxygen against the tensions of this gas in the body fluids. (About 0.2 atmosphere for arterial blood.) Evidently, the swimbladder wall must be remarkably impermeable to oxygen.

MECHANICAL PROPERTIES OF THE SWIMBLADDER WALL

Apart from Alexander's (1959*a, b, c*) studies of the swimbladder wall of cyprinid and other fishes, little is known of the physical properties of this tissue-complex. In cyprinids the posterior chamber of the swimbladder is remarkably inextensible, a property that is related to the high collagen content of the walls: the anterior chamber is more extensible (Alexander, 1959*b*). The swimbladders of pike and trout are much more extensible and much weaker than cyprinoid swimbladders (Alexander, 1959*c*). Judged by their fine structure, this is also true of the swimbladders of bathypelagic fishes in comparison with those of cyprinids.

Some preliminary notion of the physical properties of the swimbladder wall can be deduced from the observations of Scholander, Claff, Teng and Walters (1951) and Jones (1952). These workers considered how far a closed swimbladder might restrict rapid vertical movement in a fish above a certain level—the level at which it was in hydrostatic equilibrium. Scholander and his colleagues suggested that a fish would not move upwards beyond a level involving more than a 25 per cent change in the volume of its swimbladder, which is in good agreement with Jones's figure of 22 per cent.

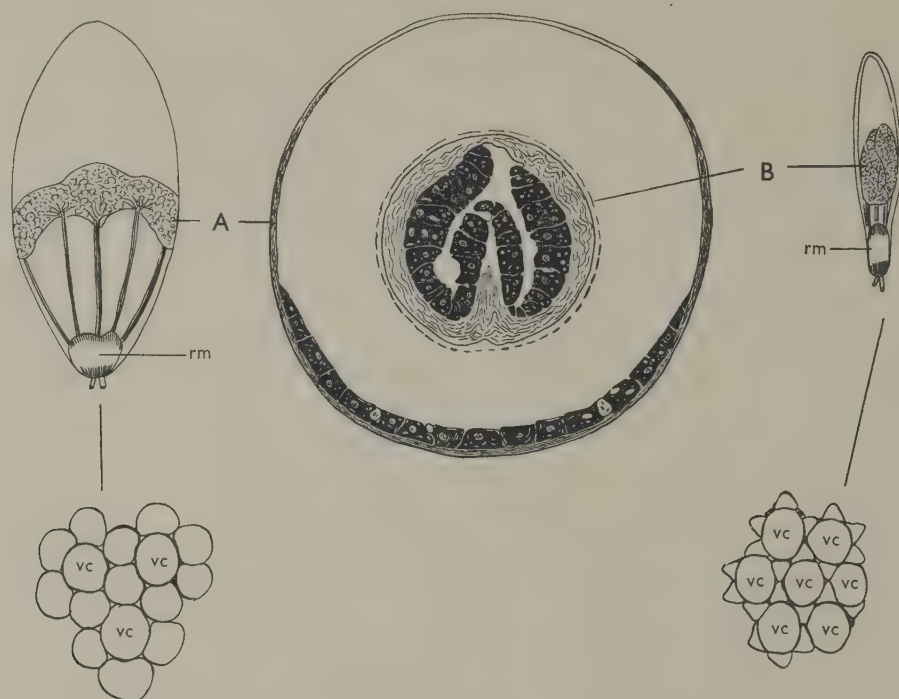
An increase of 25 per cent in the volume of a swimbladder will not lead to more than a moderate extension of the walls. As this figure may well apply to deep-water pelagic fishes, we may briefly consider what would happen to the ellipsoidal swimbladder of a myctophid. (A fish with a standard length of 70 mm. will have a swimbladder with a volume of about 0.25 ml.) An increase of 25 per cent in the volume will be accompanied by rather less than 10 per cent increase in the lengths of the major and minor axes, assuming the walls are uniformly elastic and the sac is free to expand.

There is a further consideration: when fully expanded, the oval is by far the thinnest part of the swimbladder of a myctophid, and during the hauling of a fish to the surface, the oval may be blown out in the form of a blister. (This condition was found in several specimens of *Myctophum punctatum* and *Diaphus rafinesquei* (see Text-fig. 15*d*). Taking an oval with the walls distorted in the form of a hemisphere, the surface area will be increased by a factor of two. If this amount of expansion can be sustained by the flimsiest part of the swimbladder, it is unlikely that the limitation of rapid upward movements is set by the range of extensibility of the walls. (In *Argyropelecus* also it is clear that the swimbladder can sustain more than a 10 per cent increase in the lengths of the major and minor axes.) The restriction is more likely to be related to the fishes' incapacity to cope with more than a certain decrease in its density, there being a limit to what can be done by compensatory movements of the fins and body.

Whatever may be the limits of extensibility, it is rare to find a bathypelagic fish with a burst swimbladder or ruptured body-wall. While it may be easy to miss a small hole in the swimbladder of a preserved fish, distension of the organ (so that the viscera are forced out of the mouth or anus) is also unusual, except perhaps in hatchet fishes (see also p. 95).

In a letter Dr F. R. Harden Jones has told me that perch (*Perca fluviatilis*) with burst swimbladders do not appear to have ruptured body-walls, although in some instances the pressure may be sufficient to evert the rectum. Out of a sample of 106 cod taken by trawl at 20 fathoms, he found 45 per cent with broken swimbladders. At greater depths (30 fathoms and above), all were broken. But there is no evidence that the swimbladder walls of vertically migrating deep-sea fishes are any tougher in relation to the size of the sac than those of perch or cod. Saupe (1939) gives 250–300 μ as the thickness of the walls in the perch, but makes no mention of the size of the fish. This may be compared with the measurements (20–300 μ) given earlier in this section, for various species of stomiatoids and myctophids. Furthermore, there is no indication that the collagenous elements in the swimbladder wall of bathypelagic fishes are more closely packed than those of shallow water species.

Perhaps these differences between perch, cod and bathypelagic teleosts have a functional rather than a mechanical basis. A cod being hauled to the surface in a trawl is subjected to pressure changes beyond those it normally experiences. This would not apply to those bathypelagic fishes which migrate upward each day to the surface-waters. However, discussion of this will best be left to the section dealing with gas resorption (pp. 78-81).



Text-fig. 32. Semidiagrammatic reconstructions of the swimbladder of *Vinciguerria* in (A) an expanded, and (B) a compressed state. Note the changes in shape of the gas-gland cells (shown black) and the retia mirabilia (*rm*). The undulating patterns in the submucosa of the compressed swimbladder may be better seen in the microphotograph in Pl. I, fig. 1. Below are shown cross-sections of the capillaries of the retia (*vc*, venous capillaries, others arterial). In those belonging to (A) both sets of capillaries are expanded, as during gas secretion: in (B) the arterial capillaries are occluded, as during gas resorption.

During the migration of a fish towards the surface, the physical properties of the swimbladder wall must be adequate to withstand any stresses that might arise. But the walls will presumably be under tension without undue strain. It would also seem likely, as we have said, that the fibres of the submucosa will lie close together within their gelatinous matrix. When the fish dives to its daytime level, certain evidence suggests that the swimbladder cannot be kept at the required volume in the face of pressure gradient (p. 91). As the swimbladder is compressed the volume of the fish will decrease and it would seem desirable that the tissues of the walls should be freely adjustable as the sac decreases in size. If, for instance, the connective tissues were 'rigid', with little play, kinks would appear in the wall which might eventually lead to one part of the delicate gas-gland being forced against another (see Text-fig. 32). However, the presence of a voluminous, semi-fluid submucosa will allow the tissues to relax in a uniform manner and so the swimbladder may keep its shape. In a large *Diaphus rafinesquei*, the swimbladder submucosa is about 150μ in thickness, and in a sac with major and minor axes of 12.0 and 7.0 mm., the volume of this tissue will be rather more than one-tenth of that of the gas.

If the sac is compressed to half its buoyant capacity, the volumes of the gaseous and gelatinous phases will differ by no more than a factor of five. This assumes that the volume of the submucosa is unchanged. But according to Le Chatelier's theorem, colloidal gels may be expected to take up more water if subjected to an increase in pressure (Johnson, Eyring and Polissar, 1954). At all events, a study of this aspect would be of interest.

Some indication of the flow-patterns in the submucosa of a compressed swimbladder was found in *Vinciguerra*. Sections were cut through two swimbladders, one of which was well expanded, the other completely relaxed. These are shown in Text-fig. 32 and Pl. I, fig. 1. The lines of flow are indicated by the undulations of the fibres in the submucosa. The great change in the shape of the gas-gland cells can also be seen. While looking at these sections I was reminded of the experiments described by Le Gros Clark (1945). An inflated rubber balloon, the surface of which was lightly oiled, was coated with a plastic material, such as gelatin or collodion. As the balloon was deflated, small elevations appeared on the surface of the plastic, each of which sent out a triradiate pattern of anticlines as the contraction proceeded. Such elevations were found in the submucosa of the relaxed swimbladder (see Pl. I, fig. 1) and under each were arches of fibres, looking not unlike the strata forming an anticline in the earth's crust.

Turning finally to the gas-proofing properties of the swimbladder wall, Fänge (1953) has clearly shown that it is the 'secretory mucosa' which is impermeable to gases. The secretory mucosa is the inner epithelium of the secretory part of the sac. During gas-production this tissue is in a relaxed state and covers the inner surface of the bladder (the resorbent part being contracted). It is hardly surprising that this should be so, for the other parts of the swimbladder carry many blood-vessels through which gases would be lost.

Evidently the inner epithelium is the 'inner tube', the connective-tissues being merely the 'tyre'.

FAT-INVESTED SWIMBLADDERS

The presence of a fat-invested swimbladder in a deep-sea fish was first discovered by Ray (1950). In her study of the peripheral nervous system of the myctophid *Lampanyctus leucopsaras*, she figures (pl. 12, fig. 30) a transverse section through the trunk at the level of the swimbladder. Like a normal gas-filled organ, it lies immediately below the kidneys and is surrounded by peritoneum, which is darkly pigmented, as is usual in deep-sea fishes. The organ is filled with reticular connective tissue having all the appearance of a system of fat-storing cells. Barham (1957) has given these further details: 'In the adult state the bladder is largely filled by fatty connective tissue. A well developed gas-gland is present and almost fills the reduced lumen, but in some specimens a gas bubble may be present.' He also records that another myctophid, *Diaphus theta*, has a similar type of swimbladder.

As already stated in the descriptive section, fat-invested swimbladders are found in a number of bathypelagic fishes. These are:

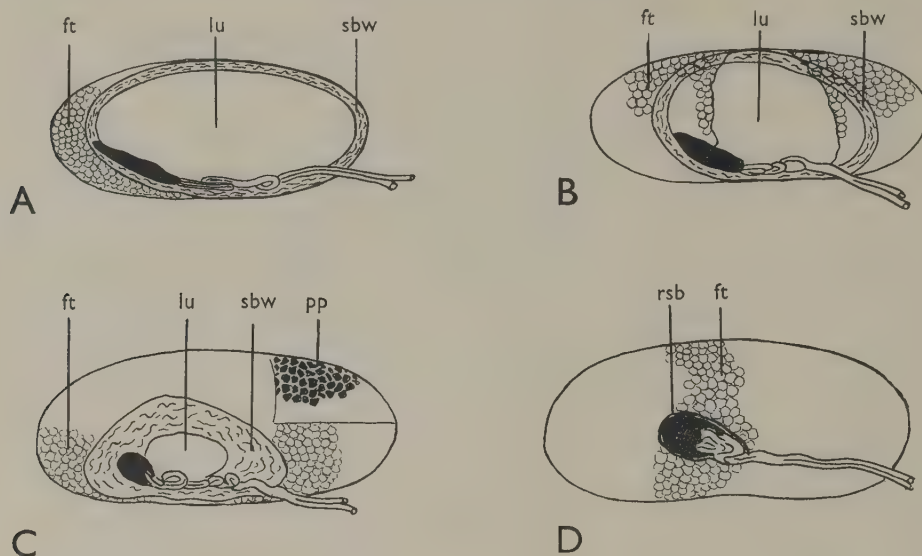
Suborder Stomiatoidea: Family GONOSTOMATIDAE, *Cyclothone* spp., *Gonostoma elongatum*; Family STERNOPTYCHIDAE, *Polyipnus laternatus*; Family ASTRONESTHIDAE, *Borostomias antarcticus*; Family STOMIATIDAE, *Stomias colubrinus*, *S. affinis*. Order Berycomorphi: Family ANOPLOGASTRIDAE, *Anoplogaster longidens*.

Kotthaus (1952) has also found a well-formed fat-bearing swimbladder in another deep-sea berycomorph, *Hoplostethus islandicus* (family Hoplostethidae).

It will thus be seen that fat-invested swimbladders are found in deep-water fishes belonging to seven different families and three orders.

As already mentioned, the post-larval stages of *Cyclothone* have a small gas-filled swimbladder. It is after metamorphosis that the swimbladder regresses and becomes invested with adipose tissue. In

Cyclothone braueri metamorphosis occurs at a length of from 11 to 14 mm. (Jespersen and Tåning, 1926), but two individuals of lengths 17 and 26.5 mm. (St. 3094, 1500(-0) m., 21. v. 54) still had no deposit of fat around the swimbladder. However, in another fish of length 26 mm. there was a small cushion of adipose tissue at the anterior end of the sac. In a 31-mm. fish the larval swimbladder had lost its ellipsoidal shape and appeared as a glistening white sphere (with a diameter of 0.6 mm.) in the middle of a blimp-shaped mass of fat, having a length of about 3 mm.



Text-fig. 33. Diagrammatic reconstructions of four stages (A-D) in the fatty investment of a regressing larval swimbladder in *Cyclothone livida*. The gas-gland is shown black. *ft*, fatty investment of swimbladder; *lu*, lumen of swimbladder; *pp*, pigmented peritoneum; *rsb*, regressed swimbladder; *sbw*, swimbladder wall.

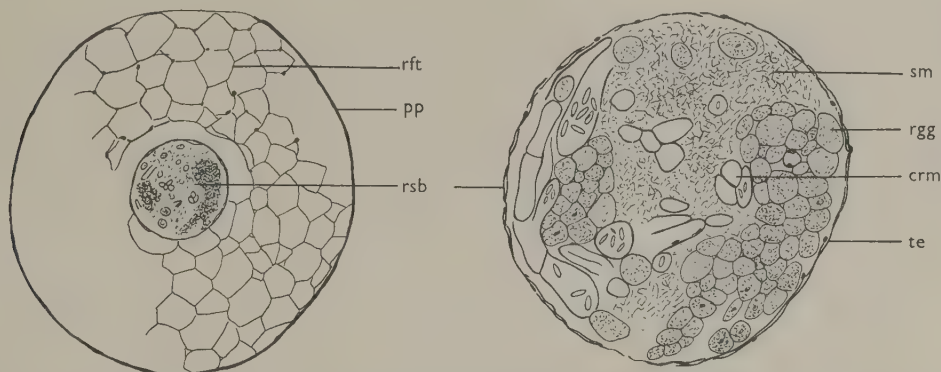
Above and below the vertical diameter of the sphere, there was only a thin covering of fat. Finally, in a 56-mm. individual the remnants of the larval swimbladder measured no more than 0.15 mm. in diameter and needed to be carefully looked for in its fatty investment. It would thus appear that the swimbladder is fully adipose in adults of about 35 mm. and upwards.

In *Cyclothone livida* (also from St. 3094) the sequence of changes is much the same and is summarized in Text-fig. 33. As in *C. braueri*, the larval swimbladder was completely regressed and surrounded by a sausage-shaped mass of fat when the fish had reached a length of about 37 mm.

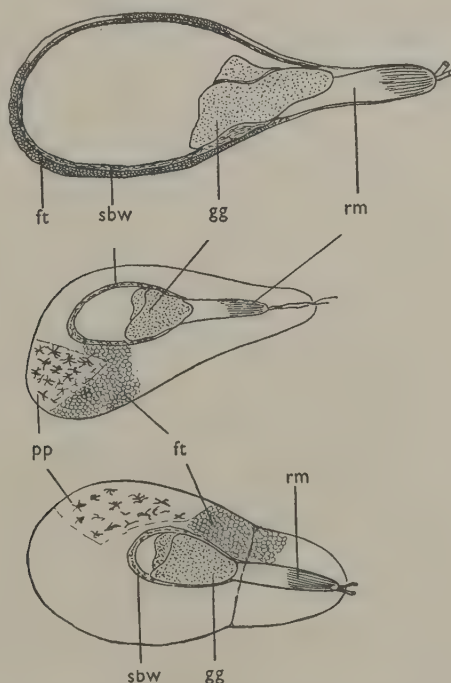
This most advanced stage in the development was examined microscopically. In Text-fig. 34 is a drawing of a transverse section at the level of the regressed swimbladder (see also Pl. I, fig. 2). The left-hand figure shows the reticular system of fat-storing cells surrounding the central regressed part of the larval swimbladder. This part is shown enlarged on the right. An outer fibrous layer encloses a mass of regressed gas-gland cells, mostly without nuclei, and the remnants of the retial capillaries. The remaining space is filled up with fine loosely-woven reticular tissue, which is undoubtedly the remains of the submucosa. The tunica externa must be represented by the outer fibrous layer, which has much the appearance of the outer circular layer fibres described by Nusbaum-Hilarowicz (1920). The mass of fat-charged cells is almost entirely bounded by the darkly pigmented peritoneum with its fine mosaic of melanophores. Thus the fat is deposited between the peritoneum and the tunica externa and in this way comes to invest the larval swimbladder as it regresses.

Varying degrees of adipose tissue investment have been found around the swimbladders of adults of the hatchet fish, *Polyipnus laternatus*. This is shown in Text-fig. 35.

The top drawing represents a swimbladder from a 32.5-mm. fish and the sac has a relatively thin layer of fat around it. The middle and lower swimbladders came from 26.5 and 33.5-mm. fishes. In these the swimbladder is buried in a mass of fat, the outline of which has some congruence to that of the sac. As in *Cyclothone*, the fat was surrounded by darkly pigmented peritoneum.



Text-fig. 34. Cross-sections through the fat-invested swimbladder of *Cyclothone livida*. On the left is shown the reticular fat-charged tissue surrounding the regressed swimbladder, which is shown enlarged on the right and has a diameter of about 300μ . *crm*, remains of capillaries of rete mirabile; *pp*, pigmented peritoneum; *rft*, reticular fatty-tissue; *rsb*, regressed swimbladder; *rgg*, regressed gas-gland cells; *sm*, submucosa; *te*, tunica externa.



Text-fig. 35. Different degrees of fat-investment of the swimbladder of *Polyipnus laternatus*. The top swimbladder ($\times 7.5$), showing the least degree of investment, is from a fish of standard length 32.5 mm. The middle one ($\times 8$) comes from a 26.5-mm. fish, while the bottom one ($\times 6$) is from a 33.5-mm. specimen. *ft*, fatty investment of swimbladder; *gg*, gas-gland; *pp*, pigmented peritoneum; *rm*, rete mirabile; *sbw*, swimbladder wall.

Compared with the swimbladder of the 32.5-mm. fish, those of the other two fishes are considerably regressed, although the main features can be clearly distinguished. It is probably significant that the dimensions of the fat body surrounding the swimbladder of the 33.5-mm. fish are much the same as those of the swimbladder of the 32.5-mm. individual. It would seem that as the swimbladder regresses, the space left between the peritoneum and tunica externa is filled with fat. But the marked difference between the swimbladders of these two equal-sized fishes suggests there must be wide variability in the stage at which this regression begins to occur.

A hydrostatic organ consisting entirely of fat is superior to one containing gas in that fats are relatively incompressible. However, fats are not much lighter than sea water, having a density of about 0.9. In a marine fish the volume of gas-filled swimbladder need only be 5 per cent of the body volume to make the fish weightless in water (Jones and Marshall, 1953). But a marine fish without such an internal float requires about 30 per cent of fat by weight for neutral buoyancy. Clearly the replacement of gas by fat is an inadequate substitution, so far as buoyancy is concerned. In *Gonostoma elongatum*, Denton and Marshall (1958) found relatively little fat, the more significant fact being that this species almost achieves neutral buoyancy by having reduced muscular and skeletal systems. But in *Cyclothone*, as will be shown later (p. 103), there is, in addition to the fat investing the swimbladder and deposited in the mesenteries, a well-developed system of fat sinuses under the skin. In a well-fed *Cyclothone* these stores of fat may occupy up to 15 per cent of the body volume (about 13 per cent of the body-weight assuming the fish to be neutrally buoyant). Again, the more significant feature, particularly in a poorly nourished fish, is the reduction of the heavy muscular and skeletal tissues.

The following conclusion seems apt: In a number of bathypelagic fishes the swimbladder regresses after metamorphosis and becomes a convenient site for the deposition of fat, but this plays a relatively small part on the 'credit' side of the 'buoyancy balance sheet'.

THE SWIMBLADDER AS A HYDROSTATIC ORGAN

The teleost swimbladder acts as a hydrostatic organ by making the fish weightless in water. Whatever movements the fish may make, whether up or down, the nervous control of the swimbladder is such that it continues to function towards this 'desirable' end. In terms of cybernetics, the 'feed-back' is arranged to steer this system towards this 'goal', the weightless condition. In other terms, here is what the fishes told the diver in one of Isak Dinesen's (1958) 'simple' stories: 'We fish rest quietly, to all sides supported, within an element which all the time accurately and unfailingly evens itself out. An element which may be said to have taken over our personal existence, in as much as, regardless of individual shape and of whether we be flatfish or roundfish, our weight and body is calculated according to that quantity of our surroundings which we displace.'

Knowing the density of the tissues (about 1.076), it can be shown that the volume of the swimbladder in a marine teleost must be about 5 per cent of the body-volume if the fish is to be in hydrostatic equilibrium with the sea (Taylor, 1921). Measurements of this percentage volume in shallow water species closely agree with this theoretical figure (Jones and Marshall, 1953). Furthermore, Kanwisher and Ebeling (1957) have found a similar agreement in bathypelagic teleosts, their measurements of the swimbladder volume in various stomiatoids, myctophids and melamphids ranging from 3.2 to 6.5 per cent of the body-volume. If deprived of their swimbladders, these deep-water fishes would need to sustain a downward force equivalent to 3.2-6.5 per cent of their weight in air in order to maintain themselves at a constant depth. Calculations made by Denton and Shaw show that the energy 'saved' can be quite appreciable (Denton and Marshall, 1958). Yet some energy is required to keep the swimbladder inflated at the appropriate volume and the amount is directly related to the

depth (Parr, 1937; Kanwisher and Ebeling, 1957), but in absolute terms this amount may be quite small (see p. 84). However, many of the bathypelagic fishes with swimbladders undertake daily vertical migrations. These will be considered in a later section (pp. 85–95). Here the main concern is with the structures involved in maintaining the swimbladder as a hydrostatic organ. These are the gas-secreting complex (rete mirabile and gas-gland) and those allowing of the loss of gases from the swimbladder (the resorbent capillary complex).

THE GAS-PRODUCING COMPLEX

The swimbladder produces gas by means of a capillary system supplying a glandular area. The gland is formed by localized modification of the epithelial cells that line the sac.

In physoclists and some physostomes (e.g. cyprinids, pike and eels) the capillaries form retia mirabilia. These consist of regular and intimate intercalations of arterial and venous capillaries, which follow parallel courses and carry blood to and from the gas-gland.¹

The retia mirabilia

Some account of the form and size of the retial system has already been given in the descriptive part of this report (pp. 7–50). In this section the emphasis will be on the fine structure.

Woodland (1911*a, b*) was the first to appreciate the essential features of retia mirabilia. He divided them into two types, unipolar and bipolar. In both kinds, an artery and vein subdivide to form the close and regular association of capillaries, (which may number many thousands), that supply the gas-gland. Before entering the gland, the retial capillaries of the bipolar type recombine to form arteries and veins, these then breaking up within the gland to form the capillary circulation. In the unipolar type the retial capillaries merely continue into the gland.

Both kinds of retia are found in the swimbladders of deep-sea fishes. All stomiatoids have a single, bipolar rete mirabile: the myctophids have three unipolar retia. Now some species of both groups live under similar hydrostatic pressures and undertake daily vertical migrations, and on this account, there would appear to be 'nothing to choose' between the efficiency of both types of system.

Apart from this consideration, it is interesting that the two most diverse groups of pelagic, deep-sea fishes, the stomiatoids and myctophids, differ in this particular way. However, it will be as well to remember Pantin's (1951) observation: that given certain standard parts, the number of structural solutions to a physiological requirement is limited by the nature and number of these parts. In this instance, given an artery and a vein that form a retial system, there would appear to be only two ways this system could feed a gas gland. The retial capillaries can either continue into the gas-gland (unipolar retia) or combine to form larger vessels (bipolar retia) before doing so.

The nature of the swimbladder as a whole must also be considered. Woodland (1911*a*) and Fänge (1953) have shown that the retia mirabilia of teleosts with a euphysoclistous swimbladder are unipolar in type. This survey has provided further evidence for this generalization. Besides the Myctophidae, the other bathypelagic euphysoclists are the Miripinnati, Anoplogastroidea, *Stylophorus* and *Chiasmodon*. All these fishes have unipolar retia. At least some of the deep-sea salmonoids are euphysoclists and their micro-retia run straight to the gas-gland. This is hardly surprising.

Apart from the stomiatoids, the only other fishes known to have bipolar retia are the eels (Apodes). The development of a bipolar retia system in the first group would appear to be linked to the venous part of the resorbent area, which drains into vessels that also supply the gas-gland. Such a circulation would hardly be feasible with the unipolar type of rete (see also p. 78). However, in both euphysoclists and eels, the secretory and resorbent parts have their own circulatory systems (Fänge, 1953).

¹ In view of this association in parallel, the noun *rete* is quite inappropriate, but the adjective is justified, for these capillary systems are wonderful instances of biological engineering in miniature. A better name would be *fascis mirabilis*.

This being so, euphysoclists simply require unipolar retia, but the eels are an exception to this 'rule'. It should also be stressed that a bipolar retial system is not a characteristic of all paraphysoclists. Unlike the stomiatoids, other teleosts with this type of swimbladder (Synentognathi and Microcyprini) have unipolar retia.

Turning now to the composition of the retia, Krogh (1922) was the first to appreciate the extraordinary extent of the capillary elements. In a cross-section of the two retia of the freshwater eel he estimated that there were 88,000 venous and 116,000 arterial capillaries. As the two retia were 4 mm. in length this gave aggregate lengths of 352 and 464 m. for the two sets of capillaries. Krogh also pointed out that the capillary elements are remarkably long compared to those in muscles, which are otherwise among the longest in the vertebrate body (e.g. 4 mm. in eel retia against 0.5 mm. in muscle).

Similar data are given in Table 3 for various species of bathypelagic fishes (see Pl. I, figs. 3 and 4 for the appearance of a rete in cross-section). The significance of the r/v ratio will become apparent in the text which follows.

Table 3. *Retial length : swimbladder volume ratios*

<i>Species</i>	<i>Number of retial capillaries</i>	<i>Retial length (mm.)</i>	<i>Total length of capillaries (m.)</i>	<i>Total r/v=retial length:volume (ml.) of sac</i>
Eel (<i>Anguilla anguilla</i>)	204,000	4.0	816.0	30
<i>Argyrops leucostictus</i>	5,000	2.0	10.0	50
<i>Polyipnus laternatus</i>	7,000	3.0	21.0	100
<i>Vinciguerria nimbaria</i>	5,000	1.0	5.0	150
<i>Myctophum punctatum</i>	2,000	2.5	5.0	20
<i>Melamphaes megalops</i>	500	12.0	6.0	30

At first sight the figures for the total lengths of the retial capillaries seem low compared with Krogh's 816 m. for the freshwater eel. But as the retia are an essential part of the gas-producing mechanism, their numerical constitution will be best regarded in relation to the volume of the swimbladder. (The volume of the eel swimbladder was estimated from Fänge's (1953) fig. 17, assuming the secretory sac to be a perfect ellipsoid.) In view of this, an r/v ratio was calculated (r being the total length of the retial capillaries, and v the volume of the swimbladder (ml.)).

While these figures can only be rough approximations, it will be seen that, except for *Polyipnus* and *Vinciguerria*, the r/v ratio of the eel is much the same as those of the bathypelagic species. And in comparing these data, it should be remembered that during its reproductive migration the freshwater eel becomes a deep-sea fish. The agreement between the ratios is thus not altogether surprising. But before considering this problem further, reference must be made to Scholander's (1954, 1958) theoretical study of the rete mirabile of deep-sea fishes.

Following earlier suggestions, Scholander convincingly argued that the retia must form a counter-current system allowing of gaseous exchange between the arterial and venous capillaries. Without intimate contact between the two sets of vessels, the blood leaving the gas-gland would be continually removing oxygen from the swimbladder. He wrote as follows in his 1958 paper (page 7):

The atmospheric oxygen which is dissolved in the sea water has a gas pressure of no more than one-fifth of an atmosphere at any depth, and the arterial pressure in the fish is slightly below this. So across the thin swimbladder wall of a fish living at a depth of 2000 m. there is a drop in oxygen pressure of nearly 200 atmospheres. The swimbladder is a living organ and is circulated with blood. At a pressure of 200 atmospheres the blood becomes charged with ten times its own volume of oxygen by simple physical solution, and if such amounts were to leave the swimbladder there would soon be no oxygen left. In more

general terms, one may state the problem thus: How can a steep concentration gradient be maintained across a barrier in spite of the fact that liquid is continuously streaming through it? The answer lies in the arrangement of the vascular channels.

Clearly, the retia will be most efficient in gaseous exchange if the capillary elements fit together so as to obtain the greatest possible surface of contact. Scholander (1954, 1958) had some interesting observations on this aspect. Transverse sections through the retia of a deep-sea eel (*Synaphobranchus*), a rose-fish (*Sebastes*) and a rat-tail (*Coryphaenoides*) showed that the arterial and venous capillaries fit together to form either a chequer-board¹ or a hexagonal star pattern. The eel has the first arrangement, one giving the maximum gaseous diffusion between the afferent and efferent capillaries, and Scholander (1954) went on to say '...it is remarkable that we find it in our deepest fish. The only other solution to the topological problem of making four polygons (black or white) meet at one point in such a way that black always borders white is realized in the hexagonal star pattern found in the rete of the rosefish' (and in that of the rat-tail).

While looking through serial transverse sections of the swimbladder of various stomiatoids, *Argyropelecus aculeatus*, *Vinciguerria nimbaria* and *Polyipnus*, I found both types of pattern in the same rete. In *Polyipnus*, for instance, there is a transition from the hexagonal to the mosaic arrangement in passing from the proximal to the distal end of the rete (see Pl. I, fig. 4). At the beginning of the rete the arterial capillaries are occluded and form an hexagonal pattern round the larger (6–8 μ) venous capillaries. About half-way down the rete, the arrangement is much the same, except that the arterial capillaries are partly open. Lastly, over the distal third of the rete, the two sets of capillaries form a mosaic pattern and are equal in size (6–7 μ). In the specimen of *Argyropelecus aculeatus*, except for a middle area at the proximal end, the rete showed a hexagonal star pattern throughout.

In a specimen of *Vinciguerria attenuata*, however, the rete of which was well expanded, the capillaries formed a mosaic pattern at all levels (see Text-fig. 32a). The seemingly curious mixture found in other stomiatoid retia is likely to be no more than a reflection of the unique arrangement whereby venous blood from the resorbent capillary bed returns through the rete (p. 79). During the secretory phase the rete will be fully expanded and both sets of capillaries will then form a mosaic pattern. When gases are being lost from the swimbladder the arterial capillaries must be closed, while the venous elements will be fully expanded. In this way a hexagonal pattern would be formed. The mixture of patterns found in some retia would thus be due to the physiological state of the fish when it died in the net. Preservation and fixation might also play some part, but evidently not in the rete of *Vinciguerria attenuata* mentioned above.

In the Myctophidae, the vascular system of the oval does not involve the retia, other than that the arterial blood may come from a branch of the retial artery. In two species, *Myctophum punctatum* and *Diaphus dofleini*, transverse sections through the retia showed the capillaries to be rounded rather than polygonal, the appearance being more like a system of condenser tubes than a mosaic. In the living fish, their shape may be otherwise.

Apart from the intimacy of their association, the total surface of contact between the capillaries will obviously be directly proportional to their length. And an increase in length will not only lead to increased exchange of gases, but also slow down the rate of blood-flow and so further enhance the efficiency of the exchange. But before considering this aspect in bathypelagic fishes, some mention must be made of Scholander's (1954, 1958) concept of the rete as a device for the building up of high pressures.

Assuming that gases are liberated from the blood, Scholander derived an equation, showing that

¹ 'Mosaic' would be a more apt descriptive term.

the equilibrium pressure is directly proportional to the diffusion across the retial capillaries and the amount of oxygen dissociated from a unit volume of blood. The inverse terms in the equation are the blood solubility coefficient for oxygen and the rate of blood-flow in the retial capillaries. Again, the longer the retial capillaries the greater the diffusion and the less the blood-flow, both of which will enhance the build-up of equilibrium pressures. Theoretically, a small difference in gas-tension in the arterial and venous capillaries at the beginning of the rete could lead to pressures of several thousand atmospheres at the end near the gas-gland. However, active secretion of oxygen by the gas-gland accords better with present knowledge than a liberation of this gas from the blood (Scholander, 1954; Sundnes, Enns and Scholander, 1958). On the other hand, the gas-gland cells might not accept oxygen from the blood unless the tension was higher than that in the swimbladder. This aspect must be left for future experiments: here we may simply remark on the significance of long capillaries for the efficient exchange of gases in the retia, particularly in those of deep-sea fishes. Regardless of the attainment of high pressures, a deep-sea fish must have well-developed retia in order to prevent the loss of gases from the swimbladder. Using his equations and reasonable values for the various constants, Scholander (1958, p. 9) calculated '... that the exchange through the rete in a deep-sea eel is so great that if the blood in swimbladder has an oxygen tension of two hundred atmospheres it will leave the bladder with an oxygen tension only a few millimetres higher than in the arterial blood'.

In proportion to the size of the swimbladder, bathypelagic teleosts have large retia mirabilia, the relative development of these systems being greater than those of shallow water species (Marshall, 1950, 1954; Jones and Marshall, 1953). This difference may be given rough quantitative expression by obtaining values of the ratio $l \times b/r$ for species from the two types of environment (l and b being the lengths of the major and minor axes of the sac (which approaches an ellipsoid in form) and r the length of the retial capillaries).

Values of this ratio are given in Table 4 (p. 74) for various species of deep- and shallow-water fishes. Drawings of the swimbladders of some of the latter species may be found in Text-fig. 36.

The first six species in the shallow-sea group are epipelagic fishes. It will be seen that the ratios in these species are far higher than the figures obtained for the deep-sea species. But as regards a counter-current exchange-system it is the absolute rather than the relative length of the retial capillaries that is significant. However, apart from *Pollichthys*, *Vinciguerria*, *Argyropelecus* and *Astro-nesthes* among the deep-sea group and *Hyporhamphus* from the epipelagic species, the retia of the bathypelagic species are longer (some much longer) than those in the surface-swimming species. And there is another factor to be considered, the diameter of the capillaries, for the smaller this is the greater the efficiency of gaseous exchange. Two of the exceptions among the deep-sea group have relatively small capillaries, which measured 7–8 μ in diameter in *Argyropelecus* and *Vinciguerria*. (There are no data for the other two.) In the epipelagic species the capillaries are 10 μ or more in diameter.

Table 4 also reveals that the ratios and retial dimensions of *Gadus minutus* and *Capros aper* are close to those of the bathypelagic species: this is not surprising in view of the depth-range of these two fishes.

Considering only the deep-sea fishes, it would be reasonable to expect that the deeper the living space the longer would be the retia. In Table 4 it will be seen that the retia of *Stephanoberyx monae* and *Melamphaes megalops* are much longer than those of the other deep-sea fishes. Now the first species may well be demersal rather than pelagic in habit and it has a depth-range extending down to 2295 m. (Grey, 1956). Norman's (1929, 1930) data for *Melamphaes megalops* suggests that this fish tends to be concentrated well below the 500-m. level. The populations of the other species tend to be centred above this depth. Even more striking instances of this correlation between the retial span and depth can be found if abyssal fishes are also considered. But this will best be left until the final section of this report.

The gas-gland

In parallel with their retia, the gas-glands of bathypelagic teleosts are relatively large compared with those of shallow-water species. Some attention has already been drawn to this (Marshall, 1950, 1954; Jones and Marshall, 1953). Here a closer comparison will be made between various epipelagic



Text-fig. 36. Swimbladders of some epipelagic and bathypelagic fishes, showing the relative developments of the retia mirabilia and gas-glands. Epipelagic species: (A, A') *Cypsilurus cyanopterus*; (B, B', B'') *Danichthys rondeletii*; (C, C') *Exocoetus volitans*; (D, D') *Petalichthys capensis*; (E, E') *Hyporhamphus* sp. Bathypelagic species: (F) *Vinciguerria attenuata*; (G) *Argyropelecus aculeatus*; (H) *Myctophum punctatum*; (J) *Chiasmodon niger*; (K) *Melamphaes megalops*. Gas-gland dotted; retia, with striations along the major axes. In A', B', B'', C', D' and E' part or the whole of the gas-secreting complex is shown enlarged. (A, $\times 0.38$; A', $\times 10$; B, $\times 0.6$; B', $\times 5$; B'', 2.5 ; C, $\times 1$; C', $\times 5$; D, $\times \frac{1}{2}$; D', $\times 5$; E, $\times 1$; E', $\times 4$; F, $\times 10$; G, $\times 10$; H, $\times 3.8$; J, $\times 6$; K, $\times 5$.)

Table 4. *Swimbladder dimensions and retial lengths of some bathypelagic and shallow-water teleosts*

Species	Length of major axis l (mm.)	Length of minor axis b (mm.)	Length of retia r (mm.)	$\frac{lb}{r}$ (ca)
Deep-sea				
<i>Gonostoma denudatum</i>	16.0	2.0	2.5	13
<i>Pollichthys maui</i>	5.0	2.0	1.2	8
<i>Bonapartia pedaliota</i>	10.0	5.0	3.6	14
<i>Vinciguerria attenuata</i>	8.5	2.75	0.8	29
<i>Argyropelecus aculeatus</i>	8.5	4.5	1.5	26
<i>Polyipnus lateratus</i>	6.0	3.5	3.0	7
<i>Astronesthes niger</i>	5.5	2.5	1.5	9
<i>Myctophum punctatum</i>	12.0	4.5	2.2	25
<i>Diaphus rafinesquei</i>	20.0	6.0	2.5	48
<i>Lampanyctus güntheri</i>	9.5	2.0	2.8	7
<i>Melamphaes megalops</i>	8.5	5.0	12.0	4
<i>Stephanoberyx monae</i>	16.0	8.0	8.0	16
<i>Chiasmodon niger</i>	16.0	3.0	3.5	14
Shallow sea				
<i>Cypsilurus cyanopterus</i>	140.0	20.0	1.5	1870
<i>Danichthys rondeletii</i>	90.0	10.0	1.25	720
<i>Exocoetus volitans</i>	58.0	6.0	1.75	200
<i>Petalichthys capensis</i>	107.0	6.0	1.0	640
<i>Hyporhamphus</i> sp.	60.0	5.0	2.5	120
<i>Scombrox saurus</i>	105.0	6.0	1.25	500
<i>Gadus minutus</i>	38.0	6.0	3.0	75
<i>Capros aper</i>	23.0	6.0	2.5	55

and bathypelagic species. The extent of the gas-glands of some of these fishes can be seen in Text-fig. 36.

While these drawings give a ready impression of the relatively large expanse of the glands in deep-sea species, a more meaningful comparison may be made by estimating the ratio of the surface-area of the gas-gland to the volume of the swimbladder. Measurements were made only on fishes showing good expansion of the gland and swimbladder, the results being given in Table 5. Before considering these figures it should be remembered that the comparison of gas-glands in terms of surface-area is not entirely appropriate, since some are more than one cell in thickness. But as the glands of the three flying fish appear to be no more than one cell thick, this will not bias the figures in favour of the deep-sea species. Of these, *Vinciguerria attenuata* and probably the two *Astronesthes*, have single layer gas-glands, while those of *Argyropelecus* and the three lantern fishes are multi-layered.

The proportionately greater glandular surface in the bathypelagic species will be immediately obvious. The contrast is as great as that between the two environments. The flying fishes spend most of their life not far below the surface, while the populations of the deep-sea species are centred at various levels between 200 and 1000 m.

The significance of these differences may be appreciated by comparing the flying-fish, *Cypsilurus cyanopterus*, with the lantern fish, *Myctophum punctatum*. A 600-g. *Cypsilurus* will have a swimbladder volume of about 30 ml., while the corresponding figure for a 5-g. *Myctophum* will be 0.25 ml. Assume that the flying fish and lantern fish live at mean pressures of 1.5 and 30 atmospheres respectively. Considering the swimbladders only during the steady state, when the gas lost by diffusion is being made up by secretion, we may further assume that the flying-fish loses 5 per cent of the contained gases during the course of a day. The same percentage may be taken for the lantern fish

for the time it spends at its daytime level (say, 12 hr.). To make good this loss, the flying-fish must secrete 1.5 ml. gas at a pressure of 1.5 atmospheres. The lantern fish must produce 0.0125 ml. at 30 atmospheres or 0.25 ml. at 1.5 atmospheres. Thus, while the volume of the flying-fish swimbladder is 120 times that of the lantern fish, the relative amounts of gas required to restore a gradual loss of buoyancy differ by no more than a factor of 6.

Table 5. *Relative development of the gas-gland in some epipelagic and bathypelagic fishes*

Species	Standard length (mm.)	Surface-area of gas-gland (mm. ²): volume of swimbladder (mm. ³)
Epipelagic		
<i>Cypsilurus cyanopterus</i>	290.0	1/120
<i>Danichthys rondeletii</i>	214.0	1/120
<i>Exocoetus volitans</i>	159.0	1/160
<i>Hyporhamphus</i> sp.	112.0	1/25
Bathypelagic		
<i>Astronesthes niger</i>	41.0	1/4
<i>A. similis</i>	104.0	1/6
<i>Vinciguerria attenuata</i>	43.5	1/7
<i>Argyropelecus aculeatus</i>	23.0	1/7
<i>Benthosema suborbitale</i>	24.0	1/2
<i>Lampanyctus giuntheri</i>	53.0	1/3
<i>Myctophum punctatum</i>	71.0	1/5
<i>Melamphaes megalops</i>	56.0	1/16
<i>Chiasmodon niger</i>	104.0	1/4

However, in estimating the figures in Table 5, it was found that a *Cypsilurus* of the above weight has a gas-gland with a surface-area of 25 mm.², while the figure for the lantern fish is about 20 mm.² Furthermore, the lantern fish has a gas-gland consisting of many layers of cells, whereas that of the flying fish is probably single-layered. This would suggest that the lantern fish is readily able to make up the loss of gas. But, unlike the flying-fish, the lantern fish undertakes extensive vertical migrations. Towards sunset it will climb several hundred metres towards the surface-layers, and after spending the hours of darkness near the surface, will then dive to its daytime depth. In considering the relative development of the gas-gland, it is clear that vertical migrations must also be taken into account. This will best be dealt with at a later stage (p. 89). Here we may turn to the fine structure of the gas-glands.

In shallow-water fishes there is considerable variability in the fine structure of the gas-glands (Woodland, 1911a; Fänge, 1953) and this is also true of deep-sea fishes. However, three main groups may be recognized (see Text-fig. 37).

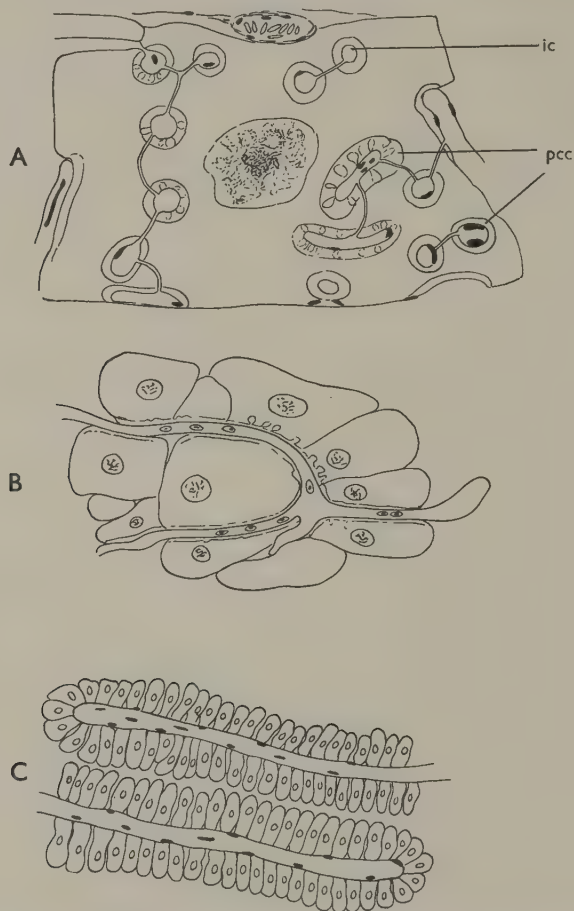
(1) Gas-glands consisting mostly of giant cells. Capillaries partly intracellular. *Vinciguerria* and *Sternoptyx*. In the first genus the cells of the expanded gas-gland measure from 100 to 150 μ in length. Nusbaum-Hilarowicz (1920) gives the dimensions of the cells of *Sternoptyx* as 50–95 μ . In *Vinciguerria* the extent of the intracellular capillaries is considerably greater than that of the intercellular elements, but the reverse seems to be true of *Sternoptyx*.

(2) Gas-glands consisting mostly of medium-sized cells. Capillaries intercellular. *Cyclothone*, 20–50 μ ; *Maurolicus*, 20–40 μ ; *Argyropelecus*, 25–50 μ ; *Polyipnus*, 25–50 μ .

(3) Gas-glands with small cells. Capillaries intercellular. *Myctophum punctatum*, 15–20 μ ; *Diaphus dofleini*, 10–15 μ ; *Opisthoproctus soleatus*, 15–25 μ .

Giant cells are also found in the gas-glands of shallow-water fishes, such as *Carapus*, *Perca* and

Zeus. In reviewing the available information, Fänge (1953) suggests that such cells may be quite common among euphysoclists. But the two genera in the first group of deep-sea fishes appear to be unique in having glands that are largely composed of giant cells. In *Vinciguerria* these cells may be as much as 100μ in depth, a striking contrast to the $10\text{--}15\mu$ cells of the gas-gland of *Diaphus dofleini*, which are disposed in several layers to a depth of about 200μ . The gas-gland of *Vinciguerria* is also remarkable in two other ways, the first being that the greater part of the contact between the giant



Text-fig. 37. Three types of gas-glands in bathypelagic fishes; (A) consisting mostly of giant cells (*Vinciguerria*), with intracellular capillaries; (B) with medium-sized cells (*Polyipnus*), and (C) with small cells (*Myctophidae*). The base of the cell of *Vinciguerria* is 170μ in length, while the cell of *Polyipnus* fitting into the U-bend of a capillary is about 50μ wide. The cells of *Myctophum* are from 10 to 17μ in length along their longer axes. *ic*, intracellular capillary; *pcc*, pericapillary cytoplasm.

cells and the capillaries supplying them is within the cytoplasm. Secondly, these intracellular capillaries connect with one another through fine canals in the cytoplasm, the lumen of the canals being little more than 1μ across, too fine to admit the elliptical red blood corpuscles, which are about $6\text{--}8\mu$ long and $2\text{--}3\mu$ wide.

A number of workers (see Fänge, 1953) have observed that the cytoplasm around the capillaries stains differently from the remaining cell contents. I have also seen this in the gas-glands of *Argyropelecus*, *Polyipnus*, *Vinciguerria*, *Maurolicus*, *Cyclothone* and *Opisthoproctus*. After staining with

haemalum and eosin, the pericapillary cytoplasm has a hyaline, homogeneous appearance, which contrasts with the lilac or salmon-pink colour of the other cell contents. The hyaline border varies from 2 to 6 μ in thickness.

In his plates of the gas-gland of *Sternoptyx*, Nusbaum-Hilarowicz (1920) shows the pericapillary borders to have a striated appearance, and this has also been reported in other fishes by Vincent and Barnes (1896) and by Bykowski and Nusbaum (1904). Like Fänge (1953), I was unable to detect this, but the sections of the giant cells of *Vinciguerria* did reveal that the interface between the blood-system and the cytoplasm can be the site of intense activity. The borders look as though they are breaking down to form small vacuoles (Pl. II, fig. 3) and this process seemed also to be taking place along the intercapillary canals in the cytoplasm. In sections of the gas-gland of *Polyipnus laternatus* the pericapillary border almost had a striated appearance, but closer examination showed the striation to be a series of elongated 'vacuoles' aligned normally to the bore of the capillaries.

These cytoplasmic inclusions cannot be gas-bubbles as they have a different optical appearance, and in *Vinciguerria*, the hyaline blobs that appear along the capillaries look very like the vacuoles that are lying free in the cytoplasm. It may also be significant that the vacuoles are generally larger near the interface between the gland cells and the swimbladder cavity.

In a series of papers, Scholander and his colleagues (Scholander and van Dam, 1954; Scholander, 1954, 1956; Sundnes, Enns and Scholander, 1958) have argued that the Root effect (the release of oxygen from oxy-haemoglobin by a lowering of the pH of the blood) plays little part in the secretion of this gas against the high oxygen pressures that exist in the swimbladders of deep-sea fishes. (By using marked oxygen (O^{18}) Scholander, van Dam and Enns (1956) showed that the gas must come from the water surrounding the fish (cod) and be transported as oxy-haemoglobin from the gills to the swimbladder).

In particular, if the lower limit of the blood pH is taken as 6.5, the Root effect is almost non-existent in deep-sea fishes, such as the long-nosed eel (*Synaphobranchus pinnatus*), the blue hake (*Antimora violacea*) and the round-nosed ratfish (*Coryphaenoides rupestris*), but is well marked in shallower-water species like the tautog (*Tautoga onitis*). (Scholander and van Dam (1954) determined the oxygen dissociation of the blood at oxygen-tensions from 0.2 to 140 atmospheres and at acidities down to pH 5.6.) Thus in deep-sea fishes the oxygen seems not to be liberated directly from the blood, but to be actively secreted by the gas-gland cells. Furthermore, even in the shallow water toadfish (*Opsanus tau*), Wittenburg (1958) has shown (in a very neat way) that the gas-gland cells are able to transport oxygen from the blood plasma into the swimbladder. After supplying the fish with carbon monoxide in (presumably) sufficient quantities to immobilize the haemoglobin, oxygen was still secreted into the swimbladder. Wittenburg suggested that this active transport of gas is by way of an iron-haem protein.

Perhaps the foregoing observations of the gas-gland cells of *Vinciguerria* also support this idea. Perhaps there are three main phases in the formation of the gas bubbles that are eventually released into the swimbladder. The first consists of an intense interaction between the blood and the pericapillary cytoplasm, when vacuoles are formed. Fänge (1953) has shown this part of the cytoplasm to be devoid of glycogen, while acid-phosphatase activity seems to be concentrated around the peripheral zones of the gland cells. The second phase would be the growth of those vacuoles and their transport to the interface between the cell and the lumen of the swimbladder. Some of the energy for this process would be provided by the breakdown of glycogen. The vacuoles may discharge their contents into the mucous fluid covering the gas-gland, after which gas bubbles are formed (third phase) eventually bursting to release their contents (mainly oxygen) into the swimbladder cavity. (Gas-bubbles have never been observed within the gland cells.) The function of the vacuoles would

be to supply 'high tension' gas-nuclei around which the bubbles could form. However, due to surface-tension, the gas-pressure within a bubble is inversely related to the diameter of the bubble, which means that considerable pressures will be required for its growth. But in the foam found in lung-alveoli, Pattle (1958) discovered that the surface-tension of the bubbles was much reduced by a surrounding layer of insoluble protein. Perhaps the foam covering the gas-gland has somewhat similar properties.

In conclusion, it must be acknowledged that little is known of gas-secretion by the swimbladder, particularly in deep-sea fishes. As Scholander (1956, p. 523) has written: 'In spite of all the information available regarding the function of the gas-gland in fishes, one may safely say that none of the three cardinal feats of the gland can as yet be explained: namely, the production of 100–200 atmospheres of oxygen, of 10–20 atmospheres of nitrogen and of 0.1–0.2 atmospheres of argon.' In the endeavour to solve these problems the giant cell gas-gland of *Vinciguerria* should provide excellent experimental material, particularly for histochemical studies.

THE RESORBENT PART OF THE SWIMBLADDER

We have already seen that the swimbladder volume of a marine teleost must be kept near or equal to some 5 per cent of the body volume. There is evidence that teleost fishes have a certain latitude of movement above a level of neutral buoyancy (Scholander, Claff, Teng and Walters, 1951; Jones, 1952), but beyond this range the fish will tend to be 'ballooned' out of control as the volume of its swimbladder (and hence its own volume) increases. Apart from the dangers of injury, an upward migration involving a threefold increase in the volume of the swimbladder means that the fish must exert (by compensatory movements) an upward force equal to about 10 per cent of its weight in air in order to make 'downwards headway' (Denton and Marshall, 1958).

During a migration towards the surface, a teleost with a closed swimbladder must reduce the volume of the sac to a manageable, just buoyant, level by loss of the contained gases to the blood. This diffusion takes place through special resorbent surfaces with a rich supply of capillaries, some account of which has been given in the earlier descriptive section (pp. 7–50). These findings can now be summarized and discussed. Other aspects will also be considered in a later section on vertical migrations.

Order *Isospondyli*, Suborder Stomiatoidea

In this group there is a close association between the resorbent system and the gas-gland, for the venous return from the capillaries is generally by way of veins running from the gland to the rete mirabile. These veins may return from the gland (*Astronesthes niger*, *Vinciguerria* and *Maurolicus*), or run along the inner edge of the gland (*Pollichthys*). *Argyropelecus* also has periglandular veins but these may also pass through the gland. (With the material available it was not possible to make a close study of these venous channels.)

The arterial capillaries of the resorbent surface are formed from a branch of the retial artery which leaves this vessel just before it flows into the rete, to run forward alongside the latter. On reaching the resorbent area, it breaks up into arterioles and capillaries, which together with the venous elements, form the resorbent complex.

Since the venous blood from this complex eventually flows through the rete mirabile, a bipolar retial system would appear to be essential. To supply the venous part of a resorbent area a unipolar rete would have to give off hundreds of separate venous capillaries, which might then have to run for considerable distances before meeting their arterial counterparts (see, for instance, *Vinciguerria*, *Maurolicus* and *Astronesthes niger*). Such an arrangement might well be functionally unbalanced

with the arterial system, particularly in fishes that make upward vertical migrations. To keep the swimbladder from over-inflation the rate of gas-removal should be high: hence the need to remove venous blood from the capillary system as quickly as possible (see also pp. 92-94).

The resorbent circulation of the stomiatoid swimbladder would appear to be unique among deep-sea fishes (perhaps also among teleosts in general). It presumably functions as follows: During gas-resorption, contraction of the arterioles forming the retial capillaries will close down the flow of arterial blood through the rete (Fänge (1953) has shown how such contraction can lead to capillary closure). As the retial artery is still open blood can only flow down the arterial branch supplying the resorbent area. Blood returning from the system will be free to flow through the rete, since the venous capillaries will be fully open (presumably they have extra room for expansion owing to the virtual closing of their arterial counterparts). During gas-secretion both sets of retial capillaries will be open and the gas-gland fully expanded. Arterial blood will now flow from the retial artery into the dilated arterioles (and so through the rete) rather than down the by-pass vessel into the resorbent system. Furthermore, when the gas-gland is expanded, the resorbent system is contracted (Fänge, 1953) and this may well lead to a stoppage of the resorbent circulation.

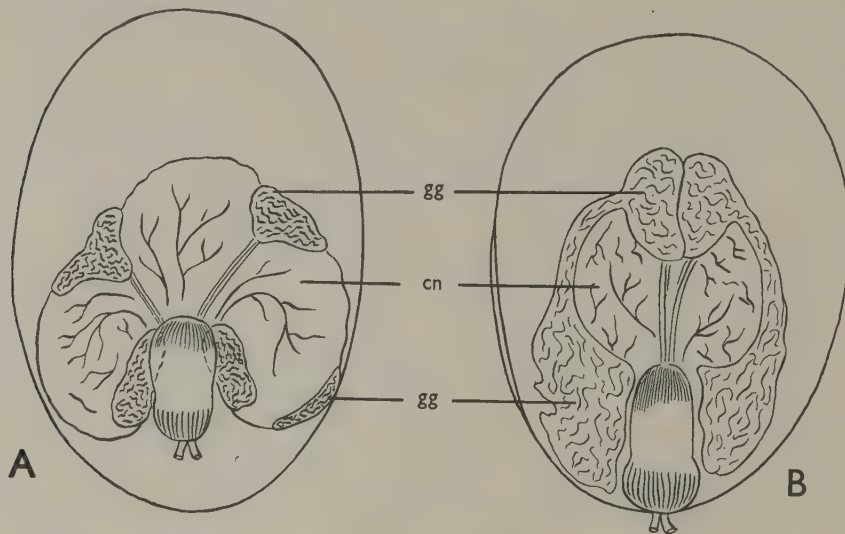
Just how this antagonistic action of the secretory and resorbent mucosa is brought about in the stomiatoids has yet to be determined. In euphysoclist teleosts, the action is perfectly clear (see p. 81 of this section). However, the smooth muscles of the swimbladder wall are likely to be involved. (In *Argyropelecus* and *Polyipnus* the muscle layer is close to the inner epithelium.) The disposition of the fibres may be such that those controlling the expansion of the capillary network are contracted during resorption, while those around the gas-gland are relaxed. The opposite would occur during gas-secretion. An extreme instance of this antagonism may be seen in Text-fig. 32 of the swimbladder of *Vinciguerria*.

Dissections made of two specimens of *Argyropelecus aculeatus* show the swimbladder as it probably appears during the resorptive and secretory phases. Considering only the former condition, the relatively large expanse of the capillary layer and the bunching up of the gas-gland is particularly striking (Text-fig. 38).

As already indicated, the capillary circulation of stomiatoids is unique in that the venous return-flow is through the rete mirabile. In the groups now to be considered the secretory part of the swimbladder is perfectly distinct from the resorbent part, this having a separate venous system (which usually runs into the hepatic or cardinal veins). Teleosts with such a swimbladder are called euphysoclists and are to be distinguished from paraphysoclists, those in which the two parts are not so sharply delimited (Rauther, 1922).

SALMONOIDEA (deep-sea). In a recent revision of the argentinine fishes (genera *Argentina* and *Glossanodon*), Cohen (1958) has shown that the swimbladder has two distinct parts, comprising an anterior, thick-walled, cylindrical chamber and a posterior, thin-walled diverticulum. From Fänge's (1958) observations and my own, it is clear that the anterior chamber contains the gas-gland and the micro-retia. Cohen described the posterior diverticulum as having a vessel from the distal end that seemed to drain into the renal portal system (or is this the dorsal aorta?), while a vein from the front of the down-turned part leads to the hepatic portal vein. In a specimen of *Argentina sphyraena* (standard length 170 mm.), I found a well-marked posterior diverticulum in which the down-turned part, that runs forward beneath the thick-walled chamber, measured 13 mm. in length. The inner epithelium of this part was thrown into folds and contained a capillary network. There is thus good indication that the diverticulum is the resorbent part of the swimbladder. I also found a thin-walled posterior chamber in *Microstoma microstoma*, but this had no down-turned antrorse section. *Nansenia* may also have such a structure (the individual I examined was not well-preserved).

In *Winteria* and *Opisthoproctus* the swimbladder does not appear to be differentiated into two sharply demarcated sections. The micro-retia and gas-gland are certainly found in the anterior part of the sac, but behind this the walls seem just as thick. Perhaps the capillary system is found in the rear part of the sac, but I was unable to ascertain this in the material at my disposal.



Text-fig. 38. Swimbladder of *Argyropelecus aculeatus*, (A) with the resorbent capillary network expanded and the gas-glands contracted, (B) with the capillary network relaxed and the gas-glands expanded. *cn*, capillary network; *gg*, gas-gland.

Order *Iniomi*, Suborder Myctophoidea

MYCTOPHIDAE. The resorbent surface of the lantern fish swimbladder is an 'oval' like that found in various gadoid, macrourid and spiny-finned fishes. It is a thin-walled circular part of the swimbladder and is surrounded by radial and circular smooth muscle fibres, having an antagonistic action. When the radial fibres contract (the circular ones being relaxed), the oval with its rich supply of capillaries is stretched and exposed to the gases in the swimbladder. The circular muscles act as a sphincter. As they contract the thick-walled parts of the swimbladder wall surrounding the oval are drawn towards its centre, eventually coming together. As the oval shuts, its walls are thrown into ridges and folds, and at the end of the process it looks like a wrinkled projection on the face of the sac.

In most of the myctophids I dissected, the oval had this appearance. It was fairly well expanded in two specimens of *Myctophum punctatum* and one of *Diaphus dofleini*, and half-open in a specimen of *D. rafinesquei* and of *Lampanyctus guentheri*. It has already been suggested that the structure Rauther (1922) described in *Diaphus rafinesquei* as the praevesica is actually an oval, and the same is presumably true of the conical projection found at the front end of the swimbladder of *Lampadena chavesi* (see pp. 38-39).

A longitudinal section of a closed oval in *Myctophum punctatum* is shown in Pl. III. At high magnifications the circular and radial muscles could be seen, the former having a 'bunched-up' appearance. The inner epithelium, close to which lies the capillary network, is thrown into folds, while the tissues in the walls have relaxed during the closure. No doubt this accommodation is made possible by the semi-gelatinous nature of the submucosa, although in the oval of the perch (*Perca fluviatilis*) Saupe (1939) found the gelatinous and fibrous components to be much reduced.

The myctophid oval lies at the anterior end of the swimbladder close to the retia mirabilia (see

Text-figs. 15-23). Its arterial supply usually comes from a branch or branches of the retial artery, while the venous return is through a vessel draining into the cardinal vein.

Order *Miripinnati*

In these teleosts the swimbladder is only functional during the larval phase (Bertelsen and Marshall, 1956). As in certain percomorph fishes, the anterior, thick-walled secretory part is sharply distinct from the posterior thin-walled section, but there is no intervening diaphragm. Although it has not been closely examined, there can be little doubt that the thin-walled part is concerned with gas-resorption.

Order *Berycomorphi*, Suborder Anoplogastroidea

Both the Melamphaidae and *Stephanoberyx* have a typical 'oval' which is set on the roof of the swimbladder near its posterior end. A drawing of the almost closed oval of a *Melamphaes megalops* is shown in Text-fig. 27. In the specimen of *M. unicornis* (Text-fig. 28) examined, the oval, from which a large vessel drains into the cardinal vein, was completely closed. The oval of the *Stephanoberyx monae* was in much the same condition as that of *Melamphaes megalops*.

Order *Percomorphi*

CHIASMODONTIDAE. *Chiasmodon niger*. In this species a diaphragm divides the anterior gas-secreting chamber from the posterior resorbent chamber. Such a partition is found in the Solenichthyes, Thoracostei, certain Percomorphi and Scleroparei (Fänge, 1953 and personal observation) and is probably quite common in zeomorph fishes (a diaphragm is found in *Zeus faber*). As Fänge (1945, 1953) has shown, the movements of this diaphragm are controlled by the antagonistic action of the secretory and resorbent parts. During gas-production the muscle fibres of the secretory part relax, while those of the resorbent mucosa are contracted. The antagonism reverses during gas-resorption. Considering first the latter, the contraction of the muscles in the secretory chamber pulls the diaphragm to the forward end of the swimbladder, while the relaxation of the resorbent layer ensures that the capillary layer is expanded and fully exposed to the gases. During secretion the diaphragm moves to the posterior end of the sac and now the gland is fully expanded.

The swimbladders of the three *Chiasmodon* examined each show different phases of this process (Text-fig. 29). In the 104-mm. fish the gland is bunched up and its chamber occupies no more than one-fifth of the total length of the swimbladder. This fraction is rather more than a half in the 49-mm. fish, while in the third fish it is a quarter. Having regard to the previous paragraph, it is evident the swimbladder of the first and third fishes show the disposition of the tissues during resorption and secretion respectively.

BATHYPELAGIC FISHES WITHOUT A SWIMBLADDER

Summarizing the earlier descriptive section, the following groups either lack a swimbladder, or it is regressed in the adult phase:

Order *Isospondyli*. Suborder Stomiatoidea: GONOSTOMATIDAE, *Cyclothone* spp., *Gonostoma elongatum*, *G. bathyphilum*; ASTRONESTHIDAE, (in *Diplolychnus mononema*, *Borostomias antarcticus*, *Astronesthes gemmifer*, the swimbladder seems to regress during adult life); STOMIATIDAE; MELANOSTOMIATIDAE; CHAULIODONTIDAE; IDIACANTHIDAE; MALACOSTEIDAE.

Suborder Salmonoidea: BATHYLAGIDAE.

Suborder Clupeoidea: ALEPOCEPHALIDAE (many of these fishes appear to be benthic in habit); SEARSIDAE.

Order *Iniomi*. Suborder Alepisauroidae. Suborder Myctophoidae: SCOPELOSAURIDAE; MYCTOPHIDAE: while most species have a swimbladder, the following species lack this organ: *Lampanyctus braueri*, *Ctenobranchus nigro-ocellatus*, *Gonichthys coccoi*, *Diaphus coeruleus*. In *Electrona antarctica*, the swim bladder regresses during the adult phase and as already mentioned (p. 65), the swimbladders of *Lampanyctus leucopsarus* and *Diaphus theta* are reduced and invested with fat.

Order *Cetunculi*, Order *Miripinnati*, Order *Giganturoidea*, Order *Lyomeri*. Order *Allotriognathi*: *Stylophorus chordatus*. Order *Berycomorphi*, Suborder Anoplogastroidea: *Anoplogaster longidens*, *Melamphaes mizolepis*. Order *Percomorphi*, CHIASMODONTIDAE: *Pseudoscopelus scriptus*, *Dysalotus alcocki*. Order *Pediculati*, Suborder Ceratioidea.

VERTICAL DISTRIBUTION AND THE SWIMBLADDER

In his 'Challenger' Report, Günther (1887, p. xxxiii) has written: 'I formerly assumed that the fishes of the open sea were living either near to the surface or at the bottom, but I think now that Mr Murray is right in supposing that certain fishes live habitually in intermediate strata, without ever coming to the surface or descending to the bottom.' The biologists of the 'Valdivia' Expedition (1898-9) were the first, however, to give close consideration to the fact that deep-sea fishes live at different levels in the ocean. After distinguishing between benthic and bathypelagic species, Brauer (1906) proceeded to discuss this problem and the difficulties involved with the use of open-nets. But the expedition did fish some closing-nets and Brauer gave examples of species taken with this gear (e.g. St. 120, *Cyclothone microdon*, 1500-900 m.; St. 227, *Sternoptyx diaphana*, 800-600 m.; St. 229, *Lampanyctus nigrescens*, 1000-800 m.). The Deutsche Südpolar Expedition (1901-3) used open vertical and horizontal nets, and some details are given of the apparent vertical distributions of the deep-sea fishes that were taken (Pappenheim, 1914).

Since these earlier expeditions, our knowledge of the depth distribution of bathypelagic fishes has been largely due to the 'Michael Sars' Expedition in 1910 (Murray and Hjort, 1912); the Danish Oceanographic Expeditions in the Mediterranean and adjacent Atlantic waters during 1908-10 (Jespersen, 1915; Tåning, 1918 and Jespersen and Tåning, 1926); the Discovery Investigations (Norman, 1929, 1930); the Dana Expeditions (Regan and Trewavas, 1929, 1930; Bertin, 1934, 1937; Ege, 1934, 1948, 1953; Bruun, 1937, Bertelsen, 1951 and Bertelsen and Marshall, 1956) and the Bermuda Oceanographic Expeditions (Beebe, 1937). From these and other publications, Grey (1956) has compiled a valuable and detailed survey of the bathypelagic and benthic fishes found below a depth of 2000 m. A more general appreciation of vertical distribution may be found in Marshall (1954).

Besides tangible evidence from the nets, underwater observations are now beginning to play their part. Since Beebe's (1934) dives in a bathysphere, a number of observers have been down in bathyscaphes. To take but one account (Pérès, 1958), it is clear that an experienced observer can both enlarge and corroborate present knowledge. During three dives off Cap Sicié, Pérès found that the schools of lantern fishes not only occurred in a mid-water layer (mainly from 400 to 700 m.), but were also clustered close to the bottom (about 10 m. above 1500 m.). He also saw that *Argyrolepecus hemigymnus* is found between 250 and 600 m. (with a maximum at 350-400 m.), which is a striking confirmation of Jespersen's (1915) estimates from open-nets.

These findings, so far as they concern the fishes dealt with in this report, may now be summarized:

A. Fishes with centres of concentration between depths of about 200 and 1000 m.

Reference to the papers cited earlier will show that any species may have a considerable vertical range about its centre of concentration. And, apart from diurnal migrations, the main depths of

occurrence may vary in space and time. Species living in very transparent waters live further down than their relatives in less clear waters (comparison of Beebe's (1937) and Grey's (1955) data with those obtained in other parts of the Atlantic (Murray and Hjort, 1912) reveals this). Furthermore, the higher the latitude the less the depth of maximum concentration (Murray and Hjort, 1912). There may also be seasonal changes, species tending to live nearer the surface during the winter months (Jespersen and Tåning (1926), Tåning (1918)).

Order *Isospondyli*. Suborder Stomiatoidea. Apart from those listed in section B, most stomiatoids seem to belong here. Suborder Salmonoidea: *Opisthoproctus*, *Winteria*, BATHYLAGIDAE. Apart from *Bathylagus argyrogastrus*, which was taken mainly above 500 m., the commoner species taken during Discovery Investigations appear to be concentrated between 500 and 1000 m. (Norman, 1930).

Order *Iniomi*. Most alepisauroids (Marshall, 1955) and Myctophidae.

Order *Giganturoidea*, Regan, 1925.

Order *Allotriognathi*, *Stylophorus chordatus* (Bruun *et al.* 1956).

Order *Berycomorphi*: MELAMPHAIDAE. The commoner species taken in Discovery nets (Norman, 1929, 1930) appear to come from depths between 500 and 1000 m.

B. *Fishes with centres of concentration between depths of about 1000 and 4000 m.*

Order *Isospondyli*. Suborder Stomiatoidea: GONOSTOMATIDAE, *Cyclothone microdon*, *C. livida*, *C. acclinidens*, *C. obscura*, *Gonostoma bathyphilum*.

Order *Lyomeri*. The centre of distribution of *Eurypharynx pelecanoides* seems to lie between 1400 and 2800 m. (Grey, 1956).

Order *Apodes*. Certain of the deep-sea eels such as *Cyema atrum*, *Serrivomer parabeani* and *Avocettina infans* appear to be commoner at these deeper levels (Grey, 1956).

Order *Berycomorphi*: *Melamphaes nigrescens* (Grey, 1956) and possibly *M. cristiceps* (Norman, 1929, 1930) occur below 1000 m.

Order *Pediculati*: Suborder Ceratioidea. Metamorphosing, adolescent and adult deep-sea angler fishes are mainly to be found at or below a depth of 1500 m. (Bertelsen, 1951).

By referring to the descriptive part of this report, it will be clear that the populations of bathypelagic fishes with fully developed gas-filled swimbladders are centred in the upper reaches (200–1000 m.) of the deep-sea. The main groups are the Gonostomatidae (most species), Sternoptychidae (hatchet fishes), *Astronesthes* spp. Myctophidae, and Melamphaidae (most species). While numerous species from these levels lack a swimbladder [the Melanostomiidae, Stomiidae, Chauliodontidae, Idiacanthidae, Malacosteidae, Bathylagidae, Alepisauroidea and Giganturoidea are the main groups (but see also the summary on p. 81–82)], this condition is universal in the fishes centred between depths of 1000 and 4000 m.

Hydrostatic pressure increases by one atmosphere for each 10 m. of depth and the average depth of the ocean is about 4000 m. It might thus be supposed that the limitation imposed on the development of a gas-filled hydrostatic organ is simply related to the pressure factor. Clearly, the aspects to be considered concern the compressibility of gases and the amounts of energy and gas required to keep the swimbladder inflated at the appropriate volume against high hydrostatic pressures.

COMPRESSIBILITY OF GASES

The swimbladder gases of deep-sea fishes consist largely of oxygen (Scholander and Van Dam, 1953; Kanwisher and Ebeling, 1957) and this gas alone will be considered.¹ At normal temperature and pressure the density of oxygen is 1.429 g./l., which value is about one seven-hundredth of the density of sea-water. In other words, at a depth of 7200 m., the density of oxygen is equal to that of seawater, and the gas would thus have lost its positively buoyant properties.

A fish having 95 g. of fat-free tissue, with a density of 1.076 (taking Taylor's (1921) estimate) and a 5-ml. swimbladder will have a density of about 1.07, which is well above the value for seawater (1.028) at this depth. Clearly a gas-filled swimbladder would be virtually useless. However, we shall see later that abyssobenthic fishes with well-developed swimbladders may range as deeply as 5000 m. At such a level the density of oxygen is about 0.7. Thus to achieve neutral buoyancy, either the volume of the swimbladder must be considerably increased or the density of the tissues be reduced. There is no evidence of the first desideratum being met, but there is good indication of a general lightening of the tissues (see p. 96).

ENERGY REQUIREMENTS OF THE SWIMBLADDER

The combined partial pressures of the gases dissolved in seawater at any depth total no more than one atmosphere. The oxygen tension is thus about one-fifth of an atmosphere, yet the partial pressure of this gas in the swimbladder may be 200 atmospheres or more (Scholander, 1954). Thus, between the uptake of oxygen by the blood circulating through the gills and its entry, under the appropriate pressure, into the swimbladder, it is clear that considerable energy will be required to concentrate the gas. By using the energy of compression equation, Parr (1937) calculated that, to fill its swimbladder to the requisite buoyant volume, a fish living at a depth of 1000 m. would use 300 times as much energy as the amount it would need at 10 m. While appreciating this, Bruun (1943) pointed out that the *absolute* amount of energy needed is quite small. He expressed it thus: 'If we take an adult *Spirula* of a weight of 10 g. and with a shell containing about 0.5 ml. gas, it would cost about 13 g. calories to fill it at 2000-m. depth, corresponding to only a few mgs of food.' Looking at the problem from much the same aspect, Scholander (1954) has calculated that for each part of oxygen secreted into the swimbladder a minimum of 3 per cent must be diverted to the work of compression. Like the compressibility factor, it would thus seem that the energy problem is not so serious as it might first appear.

GAS REQUIREMENTS OF THE SWIMBLADDER

While the proportion of oxygen needed for the energy of compression seems not to be excessive, gas must be available in sufficient quantity, if the swimbladder is to be kept inflated at the volume for weightlessness in water. The greater the depth the more the gas needed for a given unit of buoyancy (see pp. 89-90). But it should be remembered that most species of bathypelagic fishes have swimbladders with a capacity of 0.5 ml. or less. On the other hand, many of these fishes move up and down in the sea each day. As these migrations take place within the upper 1000 m. of the ocean, the effects of pressure on gas-density need not be considered. (At 500 m. the density of oxygen is about 0.07.) But as it swims downwards to regain its daytime station, the main physical stress facing a fish is the provision of enough oxygen to fill the swimbladder. From this general introduction we may turn to the physical and biological aspects of vertical migration.

¹ The swimbladder also contains nitrogen (from about 2 to 15 per cent), argon and carbon-dioxide. If the partial pressure of CO₂ ever reached 50 atmospheres, which from the papers cited, seems unlikely, it would exist as a liquid at temperatures of 13° C. and below.

THE PHYSICS AND BIOLOGY OF VERTICAL MIGRATIONS

After reviewing the evidence for the daily changes in the vertical disposition of bathypelagic fishes, some appreciation of their physical and biological environments will be given. In moving up and down, these fishes are following inner urges, and in so doing are exposing themselves to changing physical and biological conditions. Discussion of these aspects forms the third part of this section and leads to the final one, which centres around the vertical distribution of pelagic and benthic deep-sea fishes with a swimbladder.

THE EVIDENCE FOR VERTICAL MIGRATIONS

Study of the deep-sea fishes taken by the 'Challenger' (1872-6) led Günther (1887) to regard species with well-developed luminous organs and eyes as nocturnal surface-swimmers, which during the daytime, withdraw to the darkness of the deeper waters. The 'Valdivia' (1898-9) and 'Gauss' (1901-3) took numerous luminous fishes in surface-nets at night, and both Brauer (1906) and Pappenheim (1914) concluded that many deep-sea fishes regularly seek the surface-waters during the hours of darkness. The fishes they listed include several species of myctophids, *Astronesthes niger*, *Idiacanthus fasciola*, *Stomias affinis* and certain melanostomiids.

Murray and Hjort (1912) also found that *Astronesthes niger* and *Idiacanthus* could be taken at the surface during the night. Moreover, the hauls of the 'Michael Sars' enabled Hjort to be more precise concerning the vertical migrations of *Gonostoma elongatum* and *Photostomias guerni*. During the day both species were only to be found in nets fished at 500 m. and below, but at night were taken between 150 and 500 m. Jespersen (1915) was also able to analyse the diurnal changes in distribution of *Argyropelecus hemigymnus* in the Mediterranean. Daytime hauls revealed that the populations were centred below 500 m., whereas at night the main concentrations were between about 150 and 500 m.

The Dana Expeditions fished many nocturnal nets, and scrutiny of the papers concerning the fishes (Regan and Trewavas, 1929, 1930; Ege, 1934, 1948) shows that numerous stomiatoids were taken in the upper 50 m. during the night. However, many species were not caught in these near surface-nets. Considering only the former and the commoner records, the following are evidently nocturnal surface fishes: Astronesthidae: *Astronesthes niger*, *A. indicus*, *A. filifer*, Melanostomiidae: *Eustomias obscurus*, *E. brevibarbus*, *E. macrurus*, *Bathophilus metallicus*, *B. pawneeii* and *Melanostomias spilorrhynchus*; Stomiidae, all species, except *Stomias nebulosus* and *S. colubrinus*; Idiacanthidae, *Idiacanthus fasciola*; Chauliodontidae, *Chauliodus danae*, Malacosteidae, *Photostomias guerni* and *Aristostomias polydactylus*.

However, by far the commonest fishes in the surface-waters at night are the Myctophidae. Many, but seemingly not all, species can be netted at the surface after sunset. In the eastern tropical Pacific, Beebe and Vander Pyl (1944) studied the migration of various species, particularly *Gonichthys coccoi*. By day, the schools were centred about 400 m., but just after dark the fishes appeared at the surface, where they swarmed between 7.0 and 10.0 p.m. Thereafter, they appeared to disperse or withdraw from the surface, but were still caught there until 6.30 a.m., when they withdrew to their daytime levels.

The other species that massed near the surface after dark included *Lampanyctus macropterus*, *L. omostigma*, *Myctophum affine*, *M. aureolaternatum*, *M. evermanni*, *M. laternatum*, *M. reinhardti*, *Notolychnus valdiviae*. But the catches of certain species, notably *Lampanyctus mexicanus*, came from deeper-lying waters at all times of day. Other evidence for diurnal movements in Myctophidae may be found in the papers by Tåning (1918), Tucker, 1951, Grey (1956) and Barham (1957).

Besides the evidence to be got from nets, studies of fishes in relation to deep-scattering layers (Marshall, 1951; Tucker, 1951; Hersey and Backus, 1954; Kanwisher and Ebeling (1957); Backus and Barnes (1957); Johnson, Backus, Hersey and Owen (1956) and Barham (1957)) indicate that bathypelagic species, particularly those with swimbladders, are a conspicuous constituent of these layers. Furthermore, it seems likely that the most prominent of the fish sound-scatterers will prove to be myctophids. Clearly, when surer identification becomes possible, echo-sounders will provide the biologist with a valuable record of these changing events.

In conclusion, a beginning has been made on observing vertical migrations from bathyscaphes. After dives off Villefranche, Trégouboff (1958) wrote as follows: 'La plongée de nuit a permis également d'observer la migration nocturne vers la surface de divers autres animaux, tels que les Crevettes Euphausiacés, lesquelles, ayant quitté leur zone habituelle de 500 m. de profondeur environ, ont apparu en nombre à partir de 100 m. de profondeur. À leur côté chassaient activement, également à ce niveau, des petits *Argyropelecus*, qui se sont maintenus aussi nombreux jusqu'à 250 m., tandis qu'au jour on ne les capture au filet fermant qu'à partir d'au moins de 500 m. Enfin, des petits Myctophidae et quelques *Cyclothone* ont effectué également un déplacement notable vers la surface et se sont montrés, surtout les premiers, en grande quantité déjà entre 200 et 300 m. de profondeur.'

The evidence to be got from nets, sound exploration and bathyscaphes also suggests that the vertical migrations of deep-water fishes differ in extent. However, these findings will best be left until the third part of this section, when the physical problems facing fishes as they move up and down will be considered.

THE PHYSICAL AND BIOLOGICAL ENVIRONMENT

The headquarters of bathypelagic fishes are in the tropical and temperate parts of the ocean. They live below the mixed surface zone, which contains all or the greater part of the actively assimilating phytoplankton, and has an average depth of about 75 m. The lower limit of this zone is marked by a distinct thermocline, which tends to be permanent in subtropical and tropical regions, but is seasonal in temperate waters. Temperatures range from about 10° to 30° C. and salinities from about 32‰ to 41‰.

Below this thermocline comes a transition zone separating the surface mixed layer from the cold, deep water. Iselin (1936) calls this the thermocline layer, for in the warmer parts of the ocean, the temperature drops quite rapidly from about 20° C., its value just below the near-surface thermocline, to about 5° C. at about 1000 m. Taking the level of the lower thermocline to be the depth at which the rate of change of temperature is greatest, in the North Atlantic it is in this lower transition zone that the values of dissolved oxygen begin to fall towards the minimum value. But over much of the eastern tropical Pacific north of the equator, the fall in quantity of dissolved oxygen begins below the upper thermocline, and a thick oxygen minimum layer (containing less than 0.25 ml./l.) is found between depths of 100 and 1000 m. (Wooster and Cromwell, 1958). Conditions appear to be similar over the central area of the equatorial Indian Ocean, where there is an equally thick oxygen minimum layer (with values 1.0 ml./l. or less) between much the same depth-intervals (Sverdrup, Johnson and Fleming, 1942). In the Atlantic, the lowest values (1.5 ml./l. or less) are centred at a depth of about 400 m., below the North and South Equatorial currents (Riley, 1951).

Turning to submarine light, the thermocline layer contains the twilight zone of the ocean. Using a sensitive photomultiplier tube, Clarke and Wertheim (1956) were able to measure the penetration of sunlight down to depths of about 600 m. in clear water off the Western North Atlantic coast. However, the threshold of light for the eyes of many bathypelagic fishes is likely to be well below this level (Denton and Warren, 1957).

While sunlight cannot penetrate far (if at all) below this depth, there is still light from the luminous organs of deep-sea animals (Clarke, 1958). At depths between 1000 and 4000 m., temperatures range from about 6° to 1° C. in temperate and tropical regions, while the quantities of dissolved oxygen are generally above 2 ml./l.

Considering now the biological structure of temperate and tropical oceanic waters, the well illuminated surface waters (down to about 100 m.) form the living-space of the primary producers, the phytoplankton. And, except in the tropical eastern Pacific, these upper layers (from the surface down to about 200 m.) contain far greater quantities of zooplankton than the waters below (Jespersen, 1935; Vinogradov, 1955; Foxton, 1956; Zenkevitch and Birstein, 1956; Bogorov, 1958). Riley (1951) has estimated that the total oxygen consumption and phosphate regeneration below the density surface $\sigma_t = 26.5$ (average depth 200 m.) is equivalent to a utilization of about one-tenth of the surface production of organic matter by the plants. Thus, about nine-tenths of this organic production will be consumed in the upper 200 m., and, compared to the average depth of the ocean, this layer is little more than a 'surface film'.¹

While the waters below 200 m. support sparse populations of zooplankton, there is good evidence of a secondary maximum in the intermediate thermocline layer. In the western North Atlantic Leavitt (1938) found a mid-depth maximum centred at a depth of 800 m. (there was also a lower lying, but lesser concentration at 1600 m.). Jespersen (1935) also found a mid-water maximum of zooplankton (at about 1000 m.) in the tropical Pacific Ocean, whereas in the north-western part it is centred higher in the water at about 500 m. (Bogorov and Vinogradov, 1955). It would seem that the rapid increase of density and viscosity in the thermocline layer slows down the fall of detrital material, so that it tends to accumulate at mid-depths. Such concentrations of suspended material will support detritus-feeding animals and their predators. As Miyake and Saruhashi (1956) have pointed out, oxygen-minimum layers in the Atlantic and Pacific Oceans occur most frequently along the same σ_t surface (27.2–27.3) and are most marked in the more productive regions. However, in the equatorial Pacific (Albatross stations III–123, between 0° and 15° N.), Jerlov (1953) found a mid-depth maximum of suspended particles between 700 and 800 m., a level 150 m. below the centre of the oxygen-minimum layer.

Below these rather slight mid-water concentrations, the biomass of zooplankton is small until the bottom waters are reached. The concentration of plankton near the bottom has been repeatedly observed from bathyscaphes (Bernard, 1955; Pérès, Picard and Ruivo, 1957; Pérès, 1958 and Trégouboff, 1958). Apart from 'microplankton' (some of which is detritus), aggregations of larger forms, such as euphausiids, sergestids and chaetognaths have been seen. (The observations were made in the Atlantic (off Portugal) and in the Mediterranean at depths ranging from 600 to 2200 m. and the layer seems to be about 100 m. in depth.) Such near-bottom concentrations of plankton are likely to be widespread and may at least partly explain Riley's (1951) finding that the rates of oxygen consumption near the deep-sea floor appeared to be larger than those in the main body of Atlantic deep water. At all events, these bathyscaphic observations are a valuable contribution to deep-sea biology.

The time and effort given each day to vertical migrations by countless oceanic animals is one of the most striking features of their biology. But the plants can only actively assimilate carbon in the surface-waters, and the resulting marine pastures support not only the animals that occupy the same living-space, but also those in the underlying waters. Considering the fishes, there can be little doubt that their daily climb towards the surface is a feeding migration. In the western North Atlantic, to

¹ 'The autotrophic zone has a depth of 200 metres at most and includes less than 5 per cent of the volume of the ocean. Below this zone, life depends on organic matter carried down by organisms sinking from above or by the vertical migrations of animals back and forth between the depths'. Redfield (1958).

take but one instance, it is surely significant that most deep-scattering layers are detected between depths of 300 and 600 m., the levels between which Leavitt (1938) found minimum quantities of zooplankton. It seems most likely that the fishes take what food they can get during the day, but have a proper meal at night. Like the vertically migrating plankton animals, the up-and-down movements of bathypelagic fishes must be governed by the daily rhythm of submarine illumination, a rhythm that can readily be followed by their highly sensitive eyes. As Denton and Warren (1957) have shown, their pure-rod retinae contain visual gold, a pigment with enhanced sensitivity for the deeper penetrating, blue rays from the sun.

But not every species of bathypelagic fish is able to take direct advantage of the near-surface concentration of food. Adults of the deeper-living pelagic fishes (Lyomeri, ceratioid angler fishes, *Cyclothone* spp. etc.) are not found near the surface at night. This is also true of many species living in the upper 1000 m. Fishes with tubular eyes (hatchet fishes, *Opisthoproctus*, *Winteria*, *Scopelarchus*, *Evermannella*, *Gigantura*, etc.), are rarely, if ever, taken in nets fished close to the surface. It is thus evident that there are different degrees of vertical migration. These may now be summarized.

A. Bathypelagic fishes migrating upward to the surface mixed layer.

These are able to cross the thermocline and have already been mentioned in the first part of this section (p. 85-86). Certain species of the stomiatoid families, Astronesthidae, Chauliodontidae, Melanostomiatidae, Stomiidae, Iliacanthidae and Malacosteidae. Numerous species of Myctophidae.

Of the Astronesthidae, it appears that only species belonging to the genus *Astronesthes* cross the upper thermocline. It is also likely that some of the myctophids (e.g. *Lampadena* spp.) do not reach the surface-layer. The position regarding the smaller gonostomatids (e.g. *Vinciguerrria* spp., *Maurolicus* spp., *Ichthyococcus*) is less certain. While they live for the most part in the upper 500 m. and evidently undertake vertical migrations (Grey, 1955), the larger individuals are not often taken near the surface at night. Perhaps they migrate to levels close below the thermocline.

B. Partial migrators of the upper 1000 m.

Cyclothone braueri (and probably *C. signata*), Sternoptychidae, various Myctophidae, *Melamphaes* spp. Evidence for the migrations of hatchet fishes has already been given (p. 85), while Grey (1955) has noted that *Cyclothone braueri* and *Melamphaes* spp. are taken at higher levels by night than by day.

C. Deeper partial migrators

In the western North Atlantic diurnally migrating deep-scattering layers can be detected down to 1000 m. (Moore, 1958). This may well be near the threshold of light for the highly sensitive eyes of deep-water fishes (see above). In discussing this problem, Clarke (1958) wrote as follows: 'A depth of about 900 to 1000 m. would appear to be the shallowest level in clear water at which day and night changes in illumination would be below the threshold of perception and at which daylight would never be sufficiently strong for the inhabitants to be seen by their predators or by their prey.' Diurnal migrations geared to submarine sunlight would thus seem to be confined to the upper 1000 m. of the subtropical and tropical ocean. In temperate waters the threshold must be nearer the surface.

But certain of the deeper-living fishes seem to undertake vertical migrations. Off Bermuda, Grey (1955) found that the daytime catches of *Cyclothone microdon* came from nets fished between 800 and 2000 m., while at night the upper level rose to 250 m. The populations of *Cyclothone pallida*, *Melamphaes microps*, *M. opisthopterus* and *M. robustus* also occupied higher levels at night. It may be that

vertical migrations were confined to these individuals that were living by day above the threshold of light. However, there is a distinct possibility that the deeper living fishes may be migrating upwards to the mid-water concentration of plankton, which is centred at levels between 500 and 1000 m. (see p. 87). Considering the plankton maximum at 800 m. in the western North Atlantic, this could mean that the diurnal movements of the fishes living below this level were taking place without the cues provided by submarine sunlight. However, it was in this area and at a depth of 900 m. that Clarke (1958) found a maximum in the frequency of luminescent flashes from deep-sea animals. Furthermore, Kampa and Boden (1957) have found a diurnal rhythm in the mean frequency of flashes from animals in a sound scattering layer in the San Diego trough. The frequency was least at midday, greatest during the twilight migration of the layer and maintained at an intermediate level during the night. If this rhythm proves to be common to all diurnally migrating, deep-scattering layers (and these occur down to at least 800 m.), it might well be the cue for the upward migrations of the deeper living fishes. Zenkevitch and Birstein (1956) visualize a ladder of migration extending to very deep levels down which organic matter produced at the surface is conveyed to the greatest depths. Perhaps luminescent light will prove to be as important as sunlight in maintaining the daily movements up and down the ladder. Recently, Nichol (1958) has estimated the maximal distance at which the light of various marine animals can be seen in seawater by eyes that can just perceive light of $1.6 \times 10^{-10} \mu \text{w/cm}^2$. In very clear water the distances vary from 6 to 170 m., and luminescent flashes have been detected down to a depth of 3750 m. (Clarke, 1958).

PHYSICAL PROBLEMS

Against this background of their physical and biological environment, we may now turn to the physical stresses that face a fish moving up and down in the water column. Clearly, these will depend on the extent of its vertical displacement. In considering the migrations of fishes with swimbladders, they may be divided as before into thermocline crossers, those that pass through the upper thermocline into the surface mixed layer, and partial migrators, those that remain below the thermocline.

THERMOCLINE-CROSSERS

Gas secretion

While fishes are diving to their daytime levels, the pressure exerted on the swimbladder gases will increase by 1 atmosphere for every 10 m. of the descent. An adult of one of the larger myctophids, e.g. (*Myctophum punctatum*) weighs about 5 g. and the capacity of its swimbladder will be about 0.25 ml. If it moves from 10 to 300 m. and produces no gas during the descent, the volume of the swimbladder will be compressed to 0.017 ml. To inflate the sac to the requisite capacity it must produce about 0.23 ml. gas at a pressure of 30 atmospheres or 6.9 ml. at one atmosphere, the pressure of dissolved gases in seawater. Supposing the fish to have an oxygen consumption of 1 ml./hr., the physical problem of secretion seems insuperable.

Using the energy of compression equation as a basis for their calculations, Kanwisher and Ebling (1957) have considered the physiological effort needed. They take a 10-g. fish with a 0.4 ml. swimbladder and an oxygen consumption of 0.4 ml./hr. Assuming that one-third of the blood circulation is available for the swimbladder and the efficiency of the secretion process is 25 per cent, they compute that 33 hr. secretion would be needed to restore buoyancy after a migration from the surface to a depth of 400 m. But judging from the movements of deep-scattering layers, the time taken for the downward migrations would be not much more than 1 hr. and (presumably) the fish will ascend again in about 12 hr.

Perhaps the figure for the oxygen consumption is too low. Job (1955) found that a 5-g. *Salvelinus fontinalis* will take up 1 ml./hr., and from his graphs the figure for a 10-g. fish would be about 1.2 ml. But the oxygen requirements of an alpine char are not necessarily those of a lantern fish. However, it is clear that lantern fishes are very active. Summing up his bathyscaphe observations, Pérès (1958) wrote the following concerning these fishes: 'Les individus sont presque sans cesse en mouvement, mais dans les directions les plus variées.' Furthermore, they have a relatively large expanse of gill surface. Using Gray's (1954) procedure, I have measured the gill-surface of two *Myctophum punctatum*, both with a weight of about 5 g. The number of gill-lamellae per millimetre of gill-filament is about 50 and the gill area per gram of body weight is 600–700 mm.² Comparing this figure with those got by Gray and those listed by Fry (1957), this lantern fish can be put among the active species with a relatively large gill surface.¹

There is a further aspect. The catches of the 'Michael Sars' led Hjort (1935) to conclude that the twilight depths of the warm Atlantic were inhabited by a Lilliputian fauna of bathypelagic fishes.² This is particularly true of the species with a swimbladder. The adults of most gonostomatids, sternoptychids, *Astronesthes* spp., myctophids and melamphoids range between 20 and 150 mm. in standard length and weigh from about 0.5 to 10.0 g.

Now the oxygen consumption of fishes does not follow the surface rule, nor is it proportionate to weight. When the logarithm of the rate of respiration is plotted against the logarithm of weight, the slope of the curve is less than unity (usually from 0.66 to 0.9). The rate of uptake of oxygen falls between surface-area and weight dependence (Fry, 1957).

Thus, the smaller the species, the greater its oxygen consumption per unit of body weight. This may not mean that extra oxygen would be available for gas secretion, but coupled with the considerable expanse of gill surface in such fishes as the myctophids and *Astronesthes* spp., the idea is not to be dismissed. At all events it is striking that the only predatory fishes with swimbladders which cross the upper thermocline are the species of *Astronesthes*,³ and there is a marked tendency for the adults of this genus to be smaller than those of other predatory stomiatoids (Chauliodontidae, Stomiatidae, Melanostomiatidae, Idiacanthidae and Malacosteidae), which as we have seen, have no swimbladder.

Lastly, hydrostatic pressure has an effect on the rate of metabolism. Fontaine (1930) experimented on *Pleuronectes platessa*, *Ammodytes lanceolatus*, *Gobius minutus*, and *Anguilla anguilla*, finding that an increase in pressure from the atmospheric level to 100 kg./cm.² (1 kg./cm.² = 0.968 atm.) enhanced the rate of oxygen consumption by 35–88 per cent. The smaller the fish, the greater was this percentage increase. Using the first species, Fontaine showed that the rate of oxygen consumption steadily rose as the pressure was increased to 125 kg./cm.², but thereafter fell rapidly, the fish being killed at a pressure of 150 kg./cm.².

A myctophid or astronesthid diving to its daytime level might pass from a pressure of a few atmospheres to one of about forty or fifty. There is thus a possibility that their rate of oxygen uptake would tend to increase with depth. However, it is not certain that deep-water fishes would be influenced in the same way as shallow-water species, although *Anguilla anguilla* spends part of its life as a deep-sea fish. The question can only be decided by comparable experiments on deep-water species.

But even supposing that the oxygen consumption of a 10-g. deep-sea fish (say, a large myctophid)

¹ *Astronesthes niger*, which is also a thermocline-crosser also has about 50 gill-lamellae per millimetre of gill-filament. *Argyrolepis aculeatus*, presumably a partial migrator, has about 40.

² While nets give a limited impression of the size range of a species, bathyscaphe observations do not controvert Hjort's view.

³ *Astronesthes* spp. seem to have a decided liking for myctophids (Murray and Hjort, 1912; Beebe and Vander Pyl, 1944).

is three times the value taken by Kanwisher and Ebling (1957), the gas secretion time for a downward migration of 100 m. would still be 11 hr. At this rate the fish could just restore its buoyancy to the neutral level between the daily descent and ascent.¹ Moreover, it seems unlikely that the gland could produce oxygen fast enough to keep pace with the increasing pressure during the descent. A striking proof of this may well have been given by Hersey and Backus (1954). While following a descending deep-scattering layer they found that the resonant frequency of the reflected sound increased, as though elements in the nature of gas-bubbles were being compressed. As they remark, the bubbles were probably the swimbladders of fishes.

But if the cells of the gas-gland are able to store oxygen in a combined form, the task of restoring buoyancy would be quickened. As we have seen (pp. 73-75), the gland is highly developed in comparison with the volume of the swimbladder. If, by this means, buoyancy can be regained a few hours after the descent, the remaining hours before the ascent could be given to storing oxygen in the gland. If the cells have not reached saturation level by the time the fish is ready to ascend, it may be that some oxygen could be transported to them during the early part of the climb. Deep-scattering layers are known to rise quite slowly for several hours before sunset (see Clarke and Backus, 1956). During this time the (relative) reduction in pressure could be tolerated without the resorptive part of the swimbladder being brought into play (see pp. 96-97). Thus, while the gland would not be secreting it could be storing oxygen. These considerations are at least in keeping with present conceptions of gas-production. Scholander (1954) is inclined to think that oxygen in compound form may be stored in the gland-cells for intermittent use.

The oxygen secreted into the swimbladder comes from the water passing over the gills. How does a fish obtain enough oxygen if it lives in an oxygen minimum layer during the daytime? To take an extreme instance, and one already cited (p. 86), the oxygen level is below 0.25 ml./l. between depths of 100 and 1000 m. in the eastern tropical Pacific, north of the Equator. It is here that Beebe and Vander Pyl (1944) investigated the diurnal migrations of myctophids.

Thus, apart from the upper 100 m., the waters in this part of the ocean would seem to contain insufficient oxygen for active metabolism. (At 20° C. the oxygen consumption of the goldfish, a tolerant species, starts to fall below an oxygen content of 2.5 mg./l. (= 1.75 ml./l.) (Fry and Hart, 1948).) Apart from the other bodily processes, the maintenance of an oxygen pressure of 40 atmospheres in the swimbladder would be against a diffusion gradient of about 10,000 to 1 (Kanwisher and Ebeling, 1957). This seems a gigantic task.

Active life for fishes in this oxygen minimum layer would seem to pose a physiological dilemma. They would have to work very hard to get enough oxygen and the more active they were, the more oxygen would be required. To consume 0.5 ml. O₂ per hour, a lantern fish or *Astronesthes* would have to pass at least 3 l. of seawater over its gills (assuming that two-thirds of the dissolved oxygen would be taken up by the blood). A fish with a volume of, say 5 ml. would not be capable of pumping 1 ml. of seawater over its gills in a second, or even half this volume. In trout (volume about 900 ml.) Van Dam (1938) found the maximum ventilation-volume to be about 5 ml./sec.

Perhaps the activity of these fishes is largely suspended during the day. It was in the Eastern Tropical Pacific that a single haul of a mid-water trawl yielded over 5000 fishes, most of which were the small lantern fish, *Diogenichthys scofieldi* (Marshall, 1954). This is a phenomenal catch and one is led to wonder whether it might be due to reduced activity. Lantern fishes are not known to concentrate in great numbers in dense schools nor are they easy to catch. Daytime observations from a bathyscaphe might well be revealing.

¹ There is, of course, no certain evidence that the vertical migrations of any particular individual are carried out day after day. In an adult fish the extent of these displacements may also vary in time and space.

If the activities of these fishes are largely confined to night time, when they are swimming in the well-oxygenated surface waters, it is difficult to see how enough oxygen can be obtained to fill their swimbladders. Use of the gas-gland as an oxygen store would seem to be essential for such fishes. The problem (a most intriguing one), remains.

Gas resorption

During its daily climb towards the surface, a deep-sea fish must lose gas from its swimbladder as the hydrostatic pressure is reduced. While the physical problem is simply the converse of that faced during descent, it is a more critical one. Being overweight is presumably no handicap to a diving fish, but during the rise the swimbladder must be kept from exceeding the volume necessary for neutral buoyancy. If this is not done, the fish will lose control and start to 'balloon' upwards to the surface at an ever-increasing rate. Even predatory fishes without a swimbladder are not entirely free from this problem. Günther (1887) relates how Johnson found a gulper-eel (*Saccopharynx ampullaceus*) floating at the surface. The fish had swallowed a nine-inch, deep-sea gadoid (*Halargyreus*) '...the stomach of which was forced up into the mouth by the distended air bladder, showing how rapidly both fishes must have ascended to the surface'.

As we have seen, most of the migrating fishes with swimbladders weigh between 0.5 and 10 g. Considering once more a 5-g. fish with a swimbladder volume of 0.25 ml., a migration from a depth of 400–50 m. will cause the sac to expand to about 2.0 ml. if no gas is lost. So during the ascent, about 1.75 ml. gas, the greater part of which will be oxygen, must disappear into the blood.

Such problems have been considered by Jones (1951, 1952) and are based on experiments with perch (*Perca fluviatilis*), which, like the deep-sea fishes with swimbladders is a physoclist. Jones (1952) has calculated that a migration from 500 to 100 m. by a physoclist should extend over 34 hr. if the swimbladder is to be kept at the volume of neutral buoyancy. He suggests the difficulty could be overcome if the fish had a small swimbladder (the extra space being filled with fat), or thick, pressure-resisting walls bounding the sac, or if the rate of resorption is 20–30 times that supposed in the perch.

Considering these suggestions, the deep-sea fishes have a reduced swimbladder (compared to the perch) in that they live in a denser medium and so need less buoyant support. In freshwater fishes, the volume of the swimbladder is 8 per cent of the body volume (see Jones and Marshall, 1953). Moreover, the walls of their swimbladders are quite thin (see pp. 60–65). The rate of removal of gas from the sac must thus be high.

The quantity of gas diffusing into a capillary bed will directly depend on: (1) the area of the bed; (2) the rate of flow of blood; (3) the concentration gradient (the difference in tension between the swimbladder gases and those in the blood; (4) temperature. The rate of diffusion will also be inversely related to a 'frictional' component, the thickness and nature of the tissue through which the gases move, and on the size of the gas molecules.¹

The Lilliputian fauna of bathypelagic fishes have decidedly large expanses of capillaries relative to the volumes of their swimbladders (see the descriptive section, pp. 7–50). In Table 6 this is expressed as a ratio of surface of resorbent area : volume of swimbladder. The swimbladder volume is taken to be 5 per cent of the body volume. The surface-area of an 'oval' is readily calculated (but is a minimal value owing to some collapse of the swimbladder) since it is circular. In the stomiatoid fishes the area of the capillary bed was got by dividing it into convenient sub-areas. This will also be a minimal value.

¹ Fick's law for diffusion processes is expressed thus: $\frac{dn}{dt} = -\frac{RT}{Nf} a \frac{dc}{dx}$, where dn is the amount of substance diffusing across an area a , in time dt , dc/dx is the concentration gradient, R is the gas constant, T the absolute temperature, f the 'frictional resistance' and N the Avogadro number.

Table 6. *Resorbent surface-area : swimbladder volume ratios in various bathypelagic fishes*

<i>Species (standard length mm.)</i>	<i>Area of resorbent surface (mm.²)</i>	<i>Volume of swimbladder (ml.)</i>	<i>Resorbent area:volume ratio of swimbladder</i>
Stomiatoidea			
<i>Vinciguerria attenuata</i> (43.5)	20	ca. 0.08	250
<i>Maurolicus muelleri</i> (22.0)	1.2	0.01	120
<i>Argyropelecus aculeatus</i> (48.0)	9.0	0.06	150
<i>Astronesthes niger</i> (41.0)	15.0	0.05	300
Myctophidae	An oval		
<i>Diaphus rafinesquei</i> (70.0)	30	0.30	100
<i>Myctophum punctatum</i> (71.0)	25	0.25	100
Melamphaidae	An oval		
<i>Melamphaes mixolepis</i> (56.0)	8	0.07	115

These ratios are higher than that found in the perch (using Saupe's (1939) figure for the area of the oval). The two myctophids, the melamphaid and *Maurolicus* have ratios that are at least twice as large as that of the perch. In *Vinciguerria* and *Astronesthes* this factor is 4 and 5 respectively.

Clearly, the concentration gradient in these fishes will be much higher than that ever existing in the perch. At a depth of 500 m. the partial pressure of oxygen in the swimbladder will be some 40 atmospheres, a tension several hundred times greater than that in the blood flowing through the capillary bed. This would indicate that the rate of oxygen removal would be limited by the rate at which blood could flow through the resorbent area.

Now, in myctophids the vein or veins leading from the oval to the cardinal vein are extremely large. Furthermore, the by-pass vessel (or vessels) from the retial artery to the oval can take all the blood that would flow through the retia during gas-secretion. Text-fig. 39 shows two large veins from the oval of *Myctophum punctatum*, and they unite to form a single vessel running to the cardinal vein. In the stomiatoids the resorbent surface is also fed with blood through a by-pass of the retial artery while the venous return is through the venous capillaries of the rete (see pp. 78-79). However, the retial flow will not be a limiting factor, which may be seen by using Poiseuille's law. For a series of n parallel tubes the resistance to the flow of blood will be proportional to:

$$\frac{(\text{Length of a tube})}{(\text{Number of tubes}) \times (\text{Diameter of tube})^4}.$$

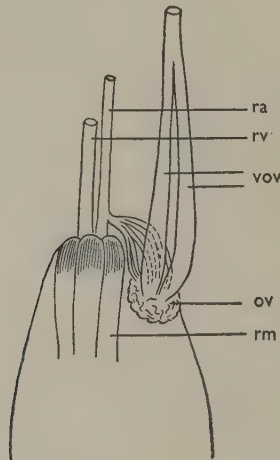
Using the figures for the diameter and length of the venous capillaries, and for the by-pass artery and other vessels involved in the capillary bed, it can be shown that the retial capillaries have less resistance than that developed in the larger vessels. It would thus seem that the resorbent vascular system in both stomiatoids and myctophids will carry relatively large amounts of blood over a given time.

Temperature will also play a part, though a small one, in accelerating the diffusion of gas into the capillary bed. In the subtropical and tropical ocean, a fish migrating from a depth of 500 m. to the surface will pass from temperatures of about 8-18° C. to those ranging from 20 to 30° C. Thus over wide areas of the warm ocean the rise in temperature is 10° C. or more. However, in terms of absolute temperature the percentage increase in diffusion rate in passing from 10° to 25° C. is less than 10 per cent.¹

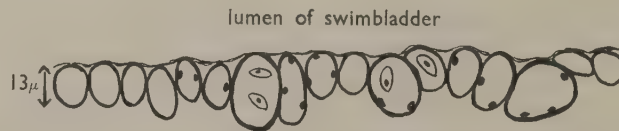
¹ Taking the rate at 20° C. as unity, the value of the diffusion constant rises 1 per cent per degree (Prosser *et al.* 1950).

Finally the 'frictional resistance' must be very small in the resorbent areas of these fishes. The capillary bed is very close to the gases of the swimbladder (Text-fig. 40), the intervening connective tissue being no more than 1μ in thickness (judging from transverse sections).

Considering only the fishes that are known to cross the near-surface thermocline, the preceding discussion could well indicate that their rate of gas resorption is 20–30 times that of the perch. They have a factor of 2–5 in their favour in resorbent surface volume of swimbladder ratio, and a factor many times this related to the concentration gradient of gas. The unknown factor is the amount of blood the resorbent surface can handle in a given time. However, judging by the ascent of deep-scattering layers (Clarke and Backus, 1956), the time taken to reach the surface (including the slow rise before sunset) is at least 2 hr.



Text-fig. 39. Venous part of the circulation to the oval in *Myctophum punctatum* ($\times 15$). Note the size of the oval veins relative to the retial vein. *ov*, oval; *ra*, retial artery; *rv*, retial vein; *rm*, rete mirabile; *vov*, veins to oval.



Text-fig. 40. Part of the resorbent capillary network of the swimbladder of *Argyropelecus aculeatus*. Note the very thin layer of tissue separating the capillaries from the lumen of the swimbladder.

PARTIAL MIGRATORS

Gas secretion

During their vertical migrations, fishes that do not penetrate beyond the upper thermocline will be subjected to lesser physical stress than those that go on to the surface mixed layer. A hatchet fish migrating from a depth of 150 to 400 m. is not faced with providing as much oxygen for the swimbladder as a lantern fish moving from 20 to 400 m. However, as we have seen (pp. 74–75) the rete and gas-gland of a hatchet fish swimbladder are highly developed, seemingly as well as those of a lantern fish. In view of the earlier discussion concerning gas-production in thermocline-crossers, this aspect need not be pursued at greater length.

Gas resorption

During its upward migration, the pressure on the same hatchet fish will be reduced by about 60 per cent; the figure for the lantern fish is about 90 per cent. It seems odd that the resorbent surface:swim-bladder volume ratio of the hatchet fish *Argyropelecus aculeatus* is greater than the values for the two lantern fishes (see Table 6). But as already suggested, the figures for the two lantern fish in Table 6 are likely to be low. If the radius of their 'ovals' was actually 4 mm. instead of 3 mm., which may well be under natural conditions, the ratios would be about 170 instead of 100. For it is a striking fact that lantern fishes brought up in nets hardly ever have the viscera pushed into the mouth by extra expansion of the swimbladder, whereas this is not uncommon in hatchet fishes. It is also interesting that *Astronesthes niger*, which appears near the surface by night, has a much higher ratio than *Argyropelecus aculeatus*, a partial migrator.

PELAGIC AND BENTHIC FISHES, THE SWIMBLADDER, AND
ASPECTS OF THE ECONOMY OF DEEP-SEA LIFE

There is a far-reaching correlation between the focal depths of the living-space and the presence or absence of a swimbladder in fishes from the mid-waters of the ocean (pp. 82-83). While a highly developed, gas-filled swimbladder is found in about half the species that swim in the upper reaches (200-1000 m.) of this environment, this organ is absent or regressed in all fishes with populations centred below the 1000-m. level. Is such a relationship with depth also found in fishes living on or near the deep-sea floor? The surprising fact, as already indicated, is that much of the answer is in the negative.

The main families to be considered are the Alepocephalidae, Bathypteroidae, Harpadontidae, Ipnopidae, Synphobranchidae*, Halosauridae*, Notacanthidae*, Moridae*, Macrouridae*, Zoarcidae, Brotulidae*, and Liparidae. In the families marked with an asterisk, a swimbladder is commonly present, but is absent in the others. Using Grey's (1956) list of species that are found below a depth of 2000 m., at least half of a total of some 240 species should have swimbladders.

Before giving special consideration to those species that range into the deeper, abyssal parts of the ocean, appreciation is due to observers in bathyscaphes and to underwater photography. Until these records were available, there was always the possibility that some of the supposedly benthic fishes might not live near the bottom. Hjort (Murray and Hjort, 1912), believed that the Bathypteroidae were mid-water fishes, but they have now been seen actually resting on the bottom, supported by the two long pectoral rays and the single, elongated caudal ray (Houot and Willm, 1955). Representatives of the Halosauridae, Moridae, Macrouridae and Brotulidae have also been observed near the bottom (Fages *et al.* 1958; Pérès, Picard and Ruivo, 1957). I have seen halosaurid, notacanthid and morid fishes in photographs of the deep-sea floor taken by Dr A. S. Laughton of the National Institute of Oceanography.

Nybelin (1957) has listed the species that have been fished below a depth of 3000 m. There are sixty-eight. (Alepocephalidae (7), Harpadontidae (2), Bathypteroidae (3), Ipnopidae (3), Synphobranchidae (3), Halosauridae (2), Notacanthidae (1), Macrouridae (16), Zoarcidae (1), Lycodidae (2), Brotulidae (25), Liparidae (3).) Thus forty-seven species may at least be suspected of having swimbladders.

However, there is the possibility that the deeper living species might have lost this organ. Yet Günther (1887) found a swimbladder in *Typhlonus nasus*, taken by the 'Challenger' at depths of 3934 and 4465 m., and in *Acanthonus spinifer*, trawled at 3242 m. Besides these two brotulids, a

swimbladder is found in the deep-sea eel *Synaphobranchus kaupi* (= *S. pinnatus*) (Scholander and Van Dam, 1954) (depth range: 200–3599 m.) and in the macrourid, *Nematonurus armatus* (Hagman, 1921) (281 to 4600 m.). 'At least forty-six of the more than seventy-six specimens recorded were caught between about 2600 and 3660 m.' (Grey, 1956).

In view of these findings I have examined the following species, the depth range¹ of which appears after the scientific name: Moridae, *Antimora rostrata* (403–2904 m.); Macrouridae, *Lionurus filicauda* (2515–4846 m.); Brotulidae, *Aphyonus gelatinosus* (2550–4360 m.); *Typhlonus nasus* (3932–5090 m.); *Mixonus laticeps* (3200–4575 m.); *Bassozetus taenia* (4575–5610 m.) and *Bassozetus compressus* (1920–2744 m.). Except in *Aphyonus gelatinosus* and *Typhlonus nasus*, each of these species has a capacious swimbladder extending down the greater part of the body cavity. Drawings of some of them appear in Text-fig. 41.

Thus a well-developed swimbladder is present in fishes that may range down to depths of about 5000 m. This is remarkable in view of the previous discussion concerning the compressibility of gases (p. 84). At a depth of 5000 m. the density of oxygen is about seven-tenths that of seawater.

A fish with a fully developed swimbladder containing oxygen would require tissues with a density of about 1.04 to be neutrally buoyant at this depth. But this requirement may well be met. These deeper-living fishes have rather lightly ossified skeletons and the muscles sheathing their flanks are fairly thin. In Pl. 3 a radiograph of *Lionurus filicauda* is shown against one of the poor cod, *Trisopterus minutus*, a shallow-water fish. It will be seen that the skeleton of the cod is more sharply revealed than that of the macrourid:² there is also a striking difference in the size of the otoliths. Denton and Marshall (1958) have shown that the density of fish muscle is relatively high, which is not surprising in view of the heavy protein molecules that are required for contraction. In bathypelagic fishes without a gas-filled swimbladder, reduction of muscle and bone can bring the animals close to neutral buoyancy.

The swimbladders of these fishes are also remarkable in having extremely long retia mirabilia (see Text-fig. 41). In *Lionurus filicauda* there are six retia, each having a length of at least 20 mm. The two retia of *Bassozetus taenia* are about 25 mm. long, while the single one of *B. compressus* has a length of 17.5 mm. In the deep-sea eel, *Synaphobranchus kaupi*, the span of the rete is about 10 mm. (Scholander, 1954).

These findings are surely significant in view of the previous discussion on retial length and the efficiency of gaseous exchange between the arterial and venous capillaries (pp. 70–72). As we saw, the deeper the living-space the longer should be the length of the capillaries. This is strikingly revealed in Table 7. (The data for *Antimora viola*, blue hake; *Sebastes marinus*, rose fish; *Nezumia bairdii*, common rat-fish; and *Synaphobranchus kaupi* are taken from Scholander and van Dam (1954) and Scholander (1954).)

Apart from the general trend, which is quite evident, it is interesting that the deeper living of the two *Bassozetus* species has the longer retia, and two in place of one. Here, then, is indication that the swimbladders of abyssal fishes may well be functional at great depths.

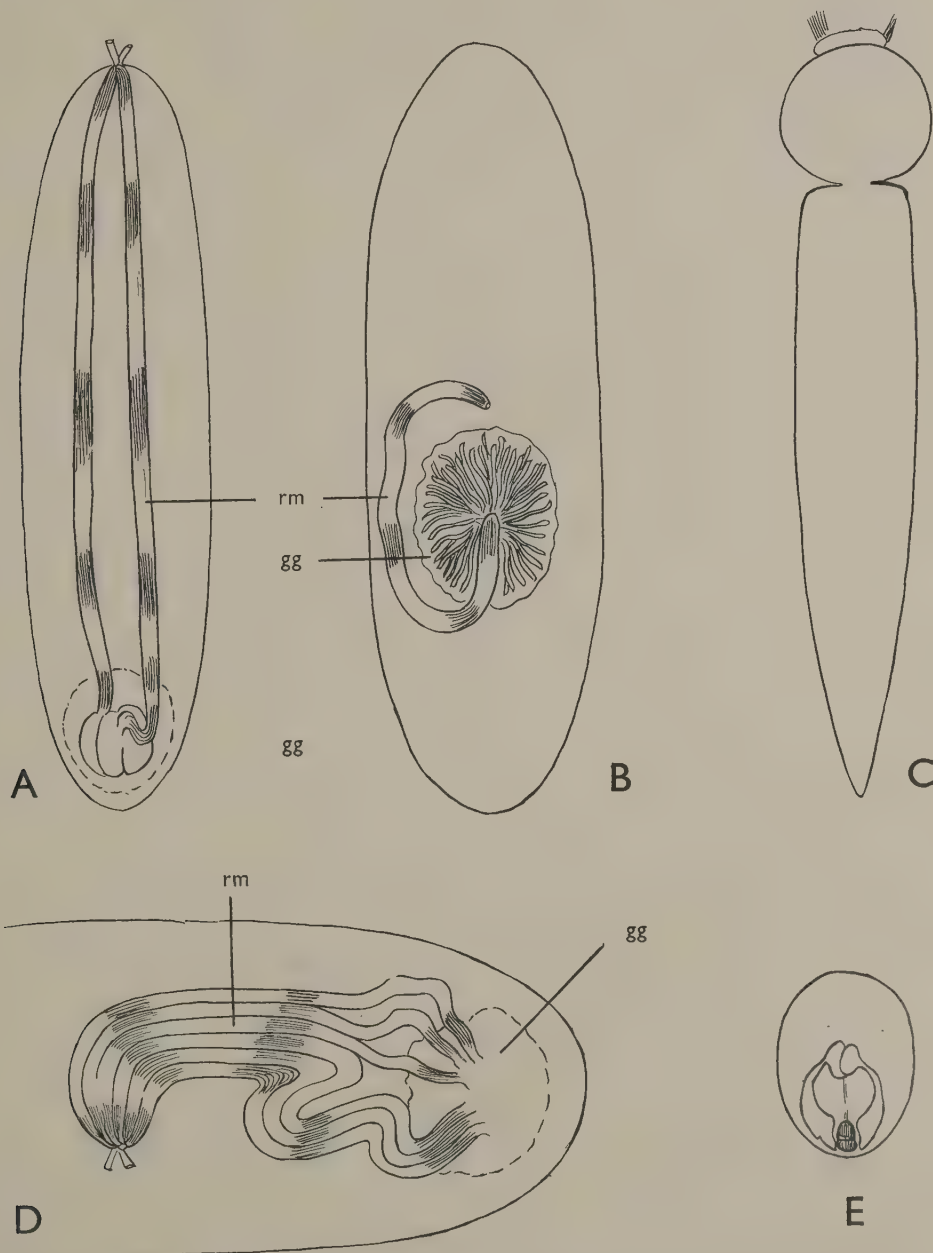
But the gas-glands do not appear to be highly developed, which might suggest that their function is simply to keep the swimbladder 'topped up' with gas. Abyssal fishes are unlikely to move very far from the deep-sea floor, except perhaps during the breeding season, although they could have a relatively wide freedom of movement in the vertical plane. If the upper limit of this zone is marked by a pressure reduction of 20 per cent (Jones, 1952), an abyssal fish with a closed swimbladder and in

¹ Depth-range data have been taken from Grey (1956), Nybelin (1957) and Bruun *et al.* (1956).

² The 'Challenger' fishes were preserved in alcohol so there is no danger of the degree of ossification being reduced.

hydrostatic equilibrium at a depth of 4000 m., could swim upwards for 800 m. without the need to lose gas. When it descended there would be no extra gas to find.

These abyssal fishes have not retained their swimbladders simply to solve problems in the second law of thermodynamics. A fish with a swimbladder is able to remain poised off the bottom without undue effort and it can thus devote a greater part of its energy to seeking its food. If a near-bottom



Text-fig. 41. Swimbladders of (A) *Bassozetus taenia*; (B) *B. compressus*; (C) *Antimora rostratus*; (D) *Lionurus filicauda*; (E) *Argyropelecus aculeatus*. In the two species of *Bassozetus* and *Lionurus filicauda*, note the extremely long retia mirabilia, which may be compared with the rete of *Argyropelecus*. Note also the capillary loops in the gas gland of *Bassozetus compressus*. gg, gas-gland; rm, rete mirabile. (A, $\times 3.6$; B, $\times 3$; C, $\times 0.7$; D, $\times 3$; E, $\times 3$.)

Table 7. *Length of retina and the depth range of some deep-sea fishes*

<i>Fishes</i>	<i>Depth range (m.)</i>	<i>Length of retina (mm.)</i>	<i>Number of retina</i>
Bathypelagic species			
Stomiatoidea	200-1000	0.75- 4.0	1
Myctophidea	(centres of concentration)	1.5 - 4.0	3
Benthic species			
<i>Sebastes marinus</i>	30-1680	7.0 -10.0	?
<i>Antimora viola</i>	560-1830	7.0 -10.0	?
<i>Stephanoberyx monae</i>	-2295	8.0	2
<i>Nezumia bairdii</i>	140-2300	7.0 -13.0	?
<i>Bassozetus compressus</i>	-2744	17.5	1
<i>Synaphobranchus kaupii</i>	200-3599	10.0	1 ?
<i>Lionurus filicauda</i>	2515-4846	20.0*	6
<i>Bassozetus taenia</i>	4575-5610	25.0	2

concentration of plankton is also found over the abyssal plain, such a fish could take full advantage of this food as well as that on and in the sediments. Macrourids plough up the oozes, no doubt in search of food, and they also take planktonic forms such as euphausiids, sergestids and copepods (Marshall, 1954). Bathypteroid fishes, which have no swimbladder and come to rest on the oozes after swimming, may be more limited in their choice. A radiograph of one of these fishes showed the skeleton to be well ossified and, as the myotomes are compact and well-developed, they are undoubtedly heavier than their environment, which as Jones and Marshall (1953) point out, is no handicap to a fish living on the bottom. But the more striking fact is that about two-thirds of the fishes that range below 3000 m. have swimbladders.

Besides its buoyant effect, the swimbladder can also be used to produce sounds. Certain species of macrourids have special drumming muscles attached to the swimbladder, but sounds can be made without such aid (Marshall, 1954). The gas-filled sac may act as a resonator to enhance the noises produced by neighbouring structures, such as the grinding of the pharyngeal teeth. In the abyssal darkness, sounds might be vitally important for communication between the sexes during the breeding season. After studying certain sounds recorded in deep water, which were like those made by fishes, Griffin (1955) suggested that the 'fish' might use the sounds for echolocation of the bottom. His concluding remarks are interesting: 'Finally it must be pointed out that even though this recording does reveal a fish-call plus its echo from the bottom, we have no direct evidence that the unknown fish could hear such an echo, and still less that it would pay any attention if it did. Yet the "echo-fish" could easily have heard these bottom echoes if it had an auditory sensitivity equal to that of any fish adequately studied to date, and in the unlighted depths of the ocean echolocation could be as advantageous to a fish as it is to a bat flying in darkness through the air.'

By becoming closely associated with the inner ears the swimbladder can also act as a hydrophone. Such association is known in one group of benthic deep-sea fishes, the Moridae, (Svetovidov, 1948) a family containing about seventy species. In other fishes a connection between the ears and swimbladder is correlated with a wide frequency range and low auditory threshold (Jones and Marshall, 1953). At present we can only add that the deep ocean is by no means a silent world.

It must now be evident that there is a striking difference between the development of the swimbladder in the pelagic and benthic fishes of the deep ocean. Taking a vertical section over the deep-sea floor between depths of 2000 and 5000 m., at least half of the pelagic fishes with centres of concentration in the upper reaches (between 200 and 1000 m.) have capacious swimbladders and the same is true of the bottom-dwelling species. But this organ is regressed or absent in the pelagic fishes living in the intervening waters below the 1000-m. level.

The evidence suggests that the swimbladder is perfectly functional in benthic species ranging beyond a depth of 2000 m. Why has this organ been lost in the deeper-dwelling pelagic fishes?

There are many differences between fishes living in the upper and lower reaches of the pelagic environment. Clearly, the most relevant contrasts may be made within genera consisting of species that inhabit both regions. *Gonostoma* is one such genus, and here *G. denudatum* will be contrasted with *G. bathyphilum*.

The populations of the first species are centred above 1000 m., while those of the second are concentrated well below this level. Certain differences between these species have already been considered (Marshall, 1954, 1955; Denton and Marshall, 1958).

Gonostoma denudatum has a capacious, gas-filled swimbladder, but there is no trace of this organ in *bathyphilum* (p. 13). Radiographs of the two fishes show the skeleton of the first species to be more heavily ossified than that of the second. Furthermore, the flanks of *denudatum* are sheathed with well-formed scales, while the skin of *bathyphilum* is naked. Correlated with the firmer skeleton, the myotomes of *denudatum* are more compact and extensive than those of *bathyphilum*. This is particularly evident along the post-anal part of the body, which is slimmer and less robust in *bathyphilum* (see Text-fig. 42).

By comparison with *bathyphilum*, the eyes and light organs of *denudatum* are highly developed. In fishes of the same size, the diameter of the eye in the former is rather less than half that of the latter, and there is a striking difference in the relative development of the dioptric parts (Marshall, 1954). Reference to Text-fig. 42 will show the extraordinary contrast in the size of the photophores.

Having proportionately larger eyes, it is not surprising that *denudatum* has larger optic lobes. But this difference in emphasis extends to all parts of the brain (see Text-fig. 42). Particular attention may be drawn to the corpus cerebellum, the volume of which in *denudatum* is about double that of *bathyphilum* (Text-fig. 42). Now there seems to be a direct correlation between the degree of development of this nervous centre and locomotor activity (see Healey, 1957; Kurepina and Pavolovsky, 1946), which would suggest that *G. denudatum* is the more active species. As we have seen, the myotomes of this species are better developed.

Parallel differences are also found in the gill-system. In *G. denudatum* the four gill-arches bear filaments along their entire length. In the specimen drawn in Text-fig. 42 the average length of the filaments on the second arch is about 2 mm., and there are some six filaments to each millimetre of the arch. The filaments bear about 60 lamellae per millimetre.

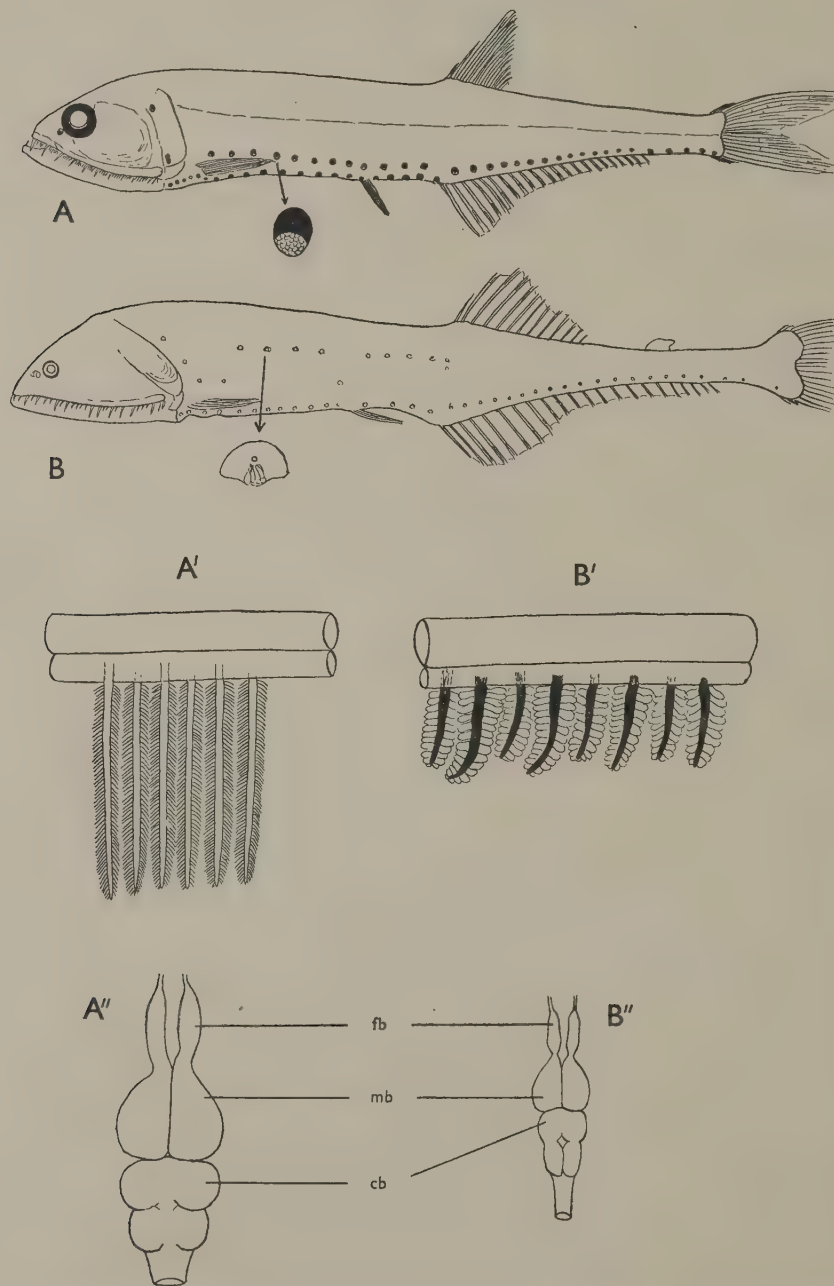
Conditions are very different in *G. bathyphilum*. On the first gill-arch the filaments are confined to the forward part of the lower arm, while on the other arches they occur along the entire extent of the lower arms. The filaments are short and feathery (about 1 mm. long and three or four per millimetre along the second arch). The number of lamellae on a 1-mm. filament is about 20–25. While there is the possibility that the skin of *G. bathyphilum*, being scaleless, might assist in respiration, there is striking indication that the tissues are much regressed by comparison with those of *G. denudatum*.

Finally, this economy of living substance in *bathyphilum* is also revealed in the size of the kidneys, which in *Gonostoma* consist of paired anterior parts joined by thin bridges of tissue to an unpaired posterior part. Comparison of a *G. bathyphilum* (standard length 77.5 mm.) with a *G. denudatum* (standard length 81.5 mm.) showed that the kidneys of the latter have a more compact appearance and are much larger than those of the former. (The anterior parts in both species have much the same length (7.0 mm.) but those of *denudatum* are more voluminous. The posterior parts of the kidneys of *denudatum* are larger by a factor of about three.)

Now in teleosts the simpler products of catabolism (ammonia and urea) tend to be excreted by the gills, while the more complex products (creatinine, creatinine and uric acid) are dealt with by the

kidneys. But as both gills and kidneys in *bathophilum* are greatly reduced, there can be little doubt that *denudatum* is the more highly organized and active species.

The species of *Cyclothone* also live at different levels in the ocean. *C. braueri*, a light-coloured species, occurs mainly between 500 and 1000 m., while the populations of the black species (*livida*,



Text-fig. 42. Comparison of the external appearance, gill development and brain of *Gonostoma denudatum atlanticum* (A, A', A'') and *G. bathophilum* (B, B', B''). The gill filaments shown in (A') and (B') are from the second gill arch. fb, forebrain; mb, mid-brain; cb, cerebellum. (A and B, $\times 0.75$; A' and B', $\times 12.5$; A'' and B'', $\times 5$.)

microdon, *acclinidens* and *obscura*) are centred at levels of 1000 m. and below. Of the forty-four recorded specimens of *obscura*, only three came from nets fished above a depth of 2000 m. (Grey, 1956), while *C. microdon* is common between levels of 1000 and 2000 m. (Murray and Hjort, 1912). We may thus compare the three species *braueri*, *microdon* and *obscura*, as they seem to occur at increasingly deeper levels.

During the larval phase, which is passed in the surface waters, a gas-filled swimbladder is present in the species *braueri* and *microdon*, but the organ regresses and becomes invested with fat after metamorphosis (pp. 65–66). Knowledge of the life-history of *obscura* matches its trivial name.

C. braueri and *C. microdon* grow to about the same size (70 mm.), but there is some evidence that the regression of the swimbladder occurs at a later stage in the former. At a length of from 30 to 35 mm., the swimbladder of *braueri* is beginning to regress but a cavity is still present, while in *C. microdon* of this size regression is almost or quite complete.

Besides this difference, which requires closer study, the degree of development of the eyes and light-organs forms a graded series in the three species. This was first appreciated by Brauer (1908) and also considered by Hjort (Murray and Hjort, 1912).¹ It will be seen that the eyes are largest in *braueri*, as compared with *microdon*, which has medium-sized eyes, while those of *obscura* are extremely small. The same is true of the photophores. It should be added that Brauer regarded the light organs of *C. obscura* to be rudimentary and found some of them to be absent.

Having no specimens of *C. obscura*, I have only been able to compare the brains of *braueri* and *microdon*, which came from individuals of about the same size (25 mm.). Drawings of these appear in Text-fig. 43. Measured from the tip of the forebrain to the end of the cerebellum, both brains have much the same length (2.0 mm.). But the optic lobes and, evidently, the cerebellum of *braueri*, are considerably larger, the width of the former being 1.1 mm. in *braueri* and 0.7 mm. in *microdon*.

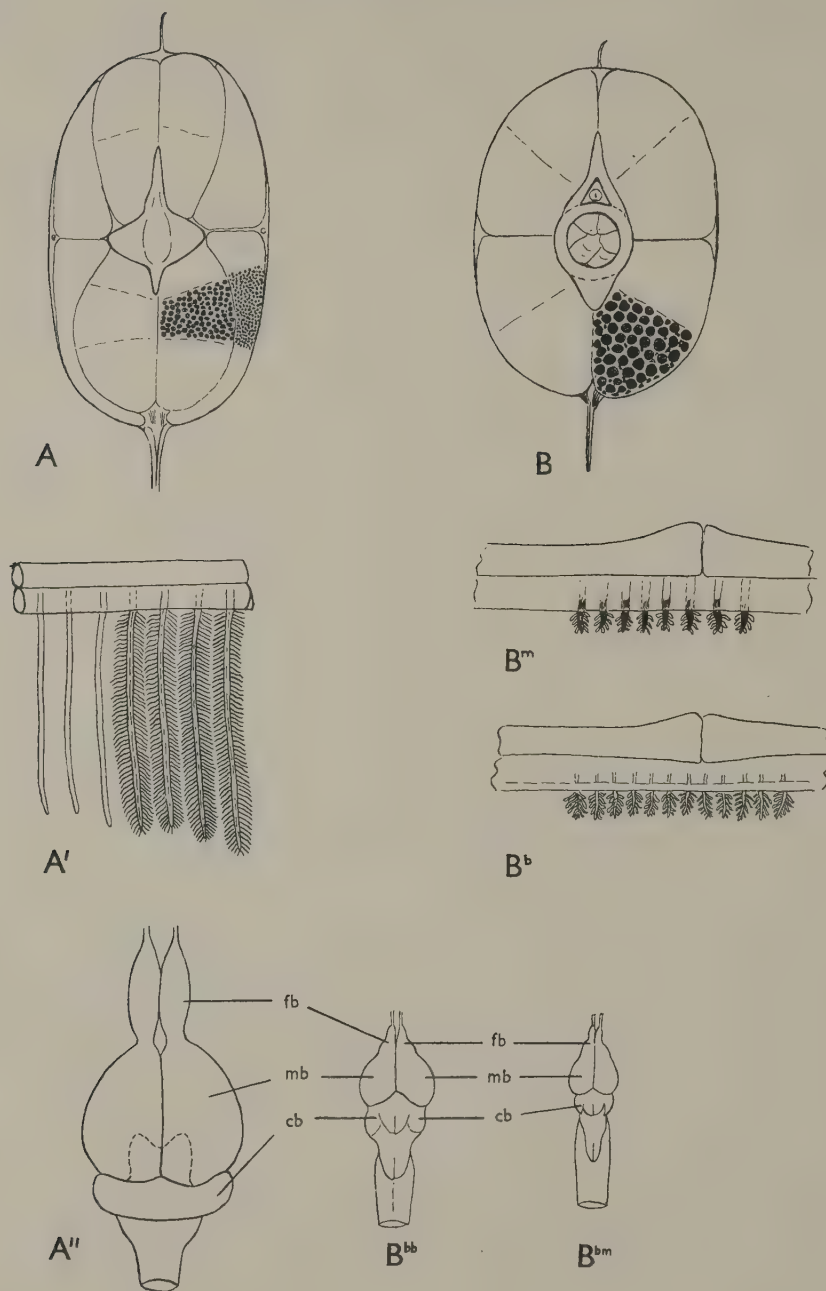
Comparison of the gill-system of these two specimens is also revealing. In both species, filaments are borne on the lower arms of the first, second and fourth arches, but on only the forward half of this part of the third arch. In *C. braueri* the filaments are both larger and more numerous, there being 12 per mm. on the first arch, compared to nine in *microdon*. Reference to Text-fig. 43 will show the difference in filament size.

To summarize, in these three species of *Cyclothone*, the deeper the living-space, the less the development of the eyes, photophores, brain and gills. Since the greater part of the populations of *C. braueri* live above the threshold of light, while both *microdon* and *obscura* are most common below this level, the relatively large eyes and photophores of *braueri* might seem to be related to an existence in the twilight zone. But this factor cannot be invoked to account for the marked difference in eye and photophore development of *microdon* and *obscura*. Some factor (or factors) related to the deeper living-space of *obscura* would seem to be involved.

To conclude these studies of related fishes, two species of the family Gonostomatidae will be considered, *Maurolicus muelleri* and *Cyclothone microdon*. *Maurolicus* is most abundant above a level of 500 m. (Koefoed, 1958) while *C. microdon*, as already indicated, is mostly to be found below 1000 m. The first species has a well-developed gas-filled swimbladder, while in *Cyclothone* this organ is obliterated in the adult phase.

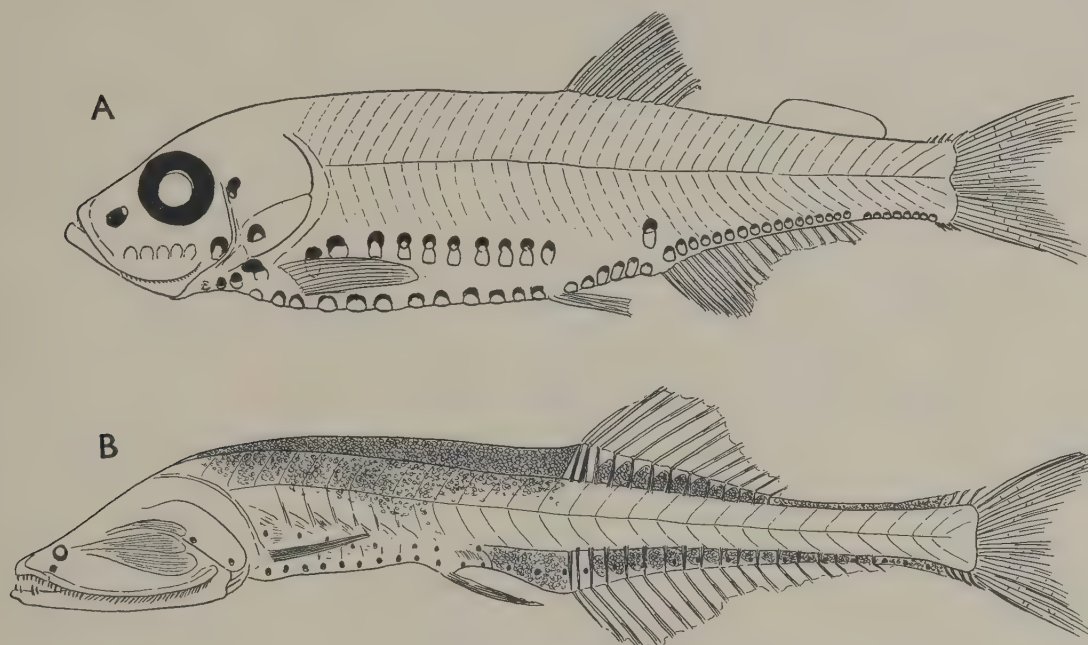
Drawings of these two fishes may be found in Text-fig. 44. The much greater development of the eyes and light-organs of *Maurolicus* will be immediately obvious. The myotomes of this fish are also much more compact and extensive. In a well-nourished *Cyclothone microdon*, the myotomes appear at first sight to be more voluminous than they actually are. Much of the space between the skin and

¹ The species that Brauer took to be *Cyclothone signata* Garman proved to be a separate species, which was called *C. braueri*, by Jespersen and Täning (1926).



Text-fig. 43. The development of the body muscles, gill filaments and brain of (A, A', A'') *Maurolicus muelleri*; (B^b, B^{bb}) *Cyclothone braueri*, and (B, B^m, B^{bm}) *C. microdon*. In A and B, which are transverse sections through the body just in front of the caudal peduncle, the muscle fibres are shown in black and are drawn to scale. The drawings of the gill filaments are from the lower part of the first gill arch. *fb*, forebrain; *mb*, midbrain; *cb*, cerebellum. (A, B, $\times 15$; A', B^m, B^b, $\times 20$; A'', B^{bb}, B^{bm}, $\times 9$.)

myotomes is taken up by extensive fat sinuses, which are especially capacious along the back between the head and the dorsal fin. Subcutaneous fat sinuses also occur between the pelvic and anal fins, between the muscles moving the dorsal and anal rays, and above and below the caudal peduncle. The drawing of the fish in Text-fig. 44B is actually of the closely related species, *C. pallida*, in which the lack of pigment in the skin makes the sinuses easier to trace.



Text-fig. 44. External appearance of (A) *Maurolicus muelleri*; (B) *Cyclothone pallida*. Both, $\times 3$.

Reference to Text-fig. 43 will show that the brain of *Maurolicus* is large compared to that of *Cyclothone microdon*. (The standard lengths of the two fishes measured 35.0 and 36.5 mm. in the order just given.) This is even more true of the gill surface. On the lower part of the first gill arch of *Maurolicus*, the filaments have an average length of 1.5 mm. and there are 5 per mm. The number of lamellae per millimetre of filament is about 50. The first two corresponding figures for *Cyclothone microdon* are 0.2 mm. and 7 per mm. Once more there is ample evidence that the species from the upper mid-waters is the more highly organized and active fish.

Apart from the greater development of the myotomes in *Maurolicus*, there is a striking difference in the nature and composition of the muscle, which may be seen in Text-fig. 43. The drawings are of cross-sections taken just in front of the caudal peduncle. Here the myotomes of *Cyclothone microdon* are formed of one type of large muscle fibre, each with a diameter of about 0.1 mm. *Maurolicus* has two types of muscle fibre. The inner parts of the myotomes consist of fibres with about half the diameter of those of *Cyclothone*, while those forming the outer parts are about half as small again. These latter are presumably red fibres.¹ As the cross-sectional area of the inner parts alone is about equal to the corresponding area of myotomes in *C. microdon*, it will be seen how much finer in texture are the muscles of *Maurolicus*. Study of the density of the fibrils in the muscle fibres of these two species would be of interest.

¹ Red muscle also forms a considerable part of the myotomes of the tunny-like fishes (Kishinouye, 1923), which are the most active of all teleosts.

It will now be clear that the body-tissues of *Cyclothone* are much reduced by comparison with those of *Maurolicus*. A striking indication of the reduced economy of life in *Cyclothone* is (again) found in the form of the kidneys, which have been studied by Owen (1938). One of his drawings is reproduced in Text-fig. 45. The entire system consists of two tubules only, which run side by side down the body-cavity and unite at the bladder. This must surely be one of the simplest kidneys in any adult fish of this size. In *Maurolicus* the kidneys are much more voluminous and have a compact appearance like those of shallow-water teleosts.

These detailed studies of related species may now be used as a guide (see Table 8) to a more general survey of the pelagic fishes living in the upper and lower reaches of the deep-sea. Here the fishes with swimbladders, species belonging to the families Gonostomatidae, Sternoptychidae, Astronesthidae and Myctophidae and having centres of concentration between depths of about 200 and 1000 m. will be compared with those of the groups Lyomeri and Ceratioidea, which have no swimbladder and are most common well below the 1000-m. level.

When these two assemblages are contrasted, the differences between them prove to be very like those between the closely related species that have just been considered. The facts may best be summarized in Table 8. The observations under the Lyomeri and Ceratioidea are based on the work of Nusbaum-Hilarowicz (1923), Bertin (1934) and Tchernavin (1947*a, b*), Waterman (1948), and Bertelsen (1951) and also on personal observation.

A few observations may be added concerning the ceratioid angler fishes. I have looked at females of *Melanocetus murrayi*, *Neoceratias spinifer* and *Danaphryne*. In all three, the first gill-arch is devoid of gill-filaments. Drawings of filaments from the second arch are shown in Text-fig. 46. In *Neoceratias* and *Danaphryne* there are no more than 50-60 gill-filaments in each gill chamber.

In the deeper living fishes, every possible economy of tissue has been developed. Compared with the species that live above them and within swimming distance of the productive surface-waters, they seem degenerate. It might be argued that the most trenchant economy has been effected by the evolution of dwarf-males in the Ceratioidea. During the free-living existence it must take much less food to maintain a male than its partner. However, there are other factors to be considered (Bertelsen, 1951).

The ceratioid angler fishes, *Cyclothone* spp., and probably the Lyomeri (*Eurypharynx* has a *leptocephalus* larva), spend their larval life in the plankton-rich surface-waters. Evidently there is not sufficient food of a suitable nature to sustain the larvae at the depths occupied by the adults. However, a good start in life must counterbalance the hazards of this type of life-history.

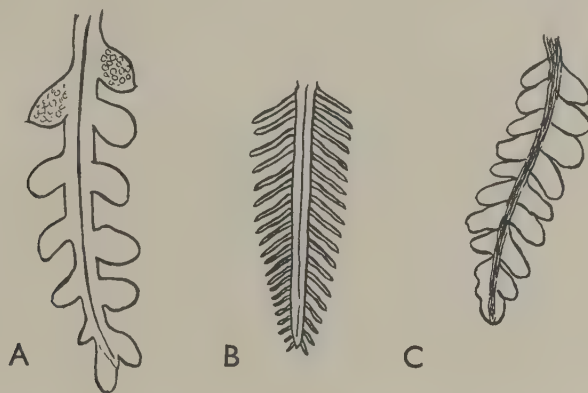
It is now well-known that the waters below 1000 m. support sparse populations of planktonic animals in comparison with the waters near the surface. The relevant papers and additional evidence



Text-fig. 45. Diagrammatic reconstruction of one of the two tubules forming the kidney of *Cyclothone* (after Owen, 1938). ($\times 7.5$.) B, bladder; G, glomerulus; P₁, P₂, first and second parts of proximal convolute; T, terminal segment.

Table 8. *The relative developments of tissue in two assemblages of bathypelagic fishes*

	<i>Gonostomatidae (most species), Sternoptychidae, Astronesthes spp. Myctophidae (most species)</i>	<i>Lyomeri and Ceratoidea¹</i>
Vertical range	200–1000 m.	1000–4000 m.
Swimbladder	Present	Absent
Skeleton	Well formed and moderately well ossified	Reduced, particularly in Lyomeri and poorly ossified
Musculature	Well developed	Reduced, particularly in Lyomeri
Eyes	Large	Relatively small (except in certain male ceratioids)
Light organs	Highly developed	Present only on female ceratioids and on tail of Lyomeri
Brain	Large, well developed	Small
Gill-system	Well developed	Much reduced

Text-fig. 46. Filaments from the second gill arch of (A) *Neoceratias spinifer*; (B) *Melanocetus murrayi*; (C) *Danaphryne* sp. (A, $\times 40$; B, $\times 20$; C, $\times 40$.)

may be found in Foxton's (1956) paper. Reference to his table 7 will show that in tropical and sub-tropical waters the mean volume of zooplankton between the surface and 150 m. is more than twenty times that between 1000 and 1500 m. In the Kurile-Kamchatka area, the biomass (mg./m.³) of plankton between the surface and 100 m. is about forty times the value measured between 1000 and 2000 m., (and about ninety times greater than that between 2000 and 4000 m.) (Zenkevitch and Birstein, 1956).

Extra data on the biomass of zooplankton in the North-western Pacific are given by Bogorov (1958). In the surface-zone (0–200 m.) the biomass is 1000 mg./m.³ or more, while in the 'transition zone' (200–500 m.), which is generally richer in species than the surface-zone, the biomass falls to about 350 mg./m.³ Below this comes a 'deep-sea zone' (500–6000 m.) in which the biomass varies from 2.64 to 78 mg./m.³ Between 6000 m. and the deep-sea floor the zooplankton-content is less than 1 mg./m.³ Finally some indication of the paucity of life in deeper waters is also given by measurements of the oxygen consumption and phosphate regeneration (Riley, 1951). Over the Atlantic (between 45° N. and 54° S.) the curves of oxygen consumption (ml./l./year) fall sharply below depths ranging from about 250 to 800 m. (see Riley's fig. 25) and Text-fig. 47 of this Report.

¹ The Giganturoidea could also be placed in this assemblage. Nearly all the sizeable specimens in the Dana collections have been taken by nets fishing below a depth of 1000 m., and, apart from their large tubular eyes, they have a low level of tissue development, much like that described under the Lyomeri and Ceratioidea. The giganturoids also have very small kidneys.

Since diurnal migrations are an integral part of the lives of so many fishes existing in the upper oceanic reaches, it is clear that they could not survive and reproduce their kind without drawing on the rich food-supply in the surface-waters. But this feeding-level is beyond the direct reach of the species living below 1000 m. Evidently the most potent environmental stress, against which they have evolved, is the sparse supply of food. But one favourable factor must have been the coolness of their surroundings: the lower the temperature the less the food required for maintaining life (Brown, 1957). On the other hand, at high hydrostatic pressures the pace of life, measured by the rate of oxygen consumption, seems to be increased (p. 90). And, while they do not have to contend with turbulent waters like the fishes that migrate to the surface-mixed layer, the laminar viscosity of the cool seas (5° C. or less) through which they must move is nearly double that at the surface in the warm ocean.

The conclusion is inescapable that the paring-down of the tissues, particularly the reduction of muscle and bone substances, is the most striking of these fishes' adaptations to their living-space. As we have seen, there is every indication that the black *Cyclothones*, ceratioid angler fishes and gulper-eels (Lyomeri) are much less active than the fishes living above them in the upper 1000 m. of the ocean. With the reduction of these tissues they have not only acquired an economy of life to match their food-supply, but have also reduced, more probably eliminated, the effort required to maintain their level in the ocean.¹ If *Gonostoma elongatum*, which also lacks a gas-filled swimbladder, comes close to neutral buoyancy (Denton and Marshall, 1958), this must surely be true of these fishes. In a well-fed *Cyclothone microdon*, the fat stored around the regressed swimbladder, attached to the mesenteries, and deposited in the subcutaneous sinuses must take up more than 10 per cent of the volume of the fish. This light tissue (with a density of about 0.9), together with the reduced muscular tissues and flimsy skeleton, may well make these fishes neutrally buoyant. In a letter to me, dated 8 November 1958, Dr Pérès has recorded his daytime bathyscaphe observations of *Cyclothone*, *Gonostoma* and *Chauliodus*. He writes: 'Ces animaux sont toujours immobiles, paraissant flotter; ils semblent attendre la proie sans la poursuivre, et il m'a été impossible de voir quelles sont les nageoires dont le mouvement aide à leur équilibre. En revanche les petits *Myctophum* sont presque toujours en mouvement.'

Cyclothone feeds on copepods and chaetognaths (Günther and Deckert, 1953), while Nusbaum-Hilarowicz (1920) found fish-scales and eye-lenses in the gut of *C. braueri*. In three individuals of *C. microdon* taken at St. 395 (48° 26½' S., 22° 10' W. to 48° 26½' S., 22° 06½' W. 13. v. 1930; N 450 H; 1500–1400 m.), I found the remains of copepods, chaetognaths, euphausiids, together with detrital material and faecal pellets. Female ceratioid angler fishes feed on organisms ranging from copepods to squids and fishes, while in the dwarf, free-living males, copepods, chaetognaths and *Phronima* have been found (Bertelsen, 1951). *Saccopharynx* takes fishes (including benthic species); *Eurypharynx*, crustaceans, worms and fishes (Bertin, 1934). The angler fishes lure their prey and certain species can master fishes several times their own length. Perhaps *Saccopharynx*, which is also a giant swallower, attracts prey by means of the spongy luminous tissue on its wisp of a tail.

Thus all these fishes, including *Cyclothone*, are predatory, and they possess jaws that are adapted for taking a very wide size-range of food organisms. If we again make the same comparisons of species from the upper and lower mid-waters, this adaptation is strikingly revealed.

¹ Certain of the deeper-living cephalopods (e.g. *Vampyroteuthis*, Cirroteuthidae, *Amphitretus* and other octopods) '... have lost most of their firmness and muscular power. They develop a thick coat of jelly-like subcutaneous tissue and the muscles themselves are sometimes degenerate and invaded by this jelly' (Morton, 1958). This parallel in the most active group of nektonic invertebrates is most striking.

Reference to Text-fig. 43 will show that *C. microdon* has much longer jaws than *Maurolicus*, the suspensoria of which are more or less vertical in position. It is clear that the diet of *Maurolicus* must be restricted, probably to organisms the size of large copepods. However, it lives nearer to good supplies of such food.

Again, *Gonostoma bathyphilum* possesses longer jaws hinged to more backwardly carried suspensoria than its relative *G. denudatum* (see Text-fig. 42). This tendency is carried to an extreme in the *Lyomeri* in which the suspensoria and jaws are many times longer than the neurocranium. Moreover, the premaxillae and maxillae have been lost, the teeth in the upper part of the mouth being carried on the palatopterygoid elements (Tchernavin, 1947a). The skeleton is also reduced in many other ways. But the most fantastic regression of bone and other tissues occurs in the Monognathidae, fishes that may well live in the same oceanic layers as the *Lyomeri* (Bertin, 1938).

The jaws, and especially the buccal cavity, of most female ceratioid angler fishes are also large. 'The length of the premaxillary and maxillary is usually more than 50 per cent of the distance from snout to end of cranium and reaches 100-150 per cent in *Caulophryne* and many *Linophrynids*' (Bertelsen, 1951).

The degree of adaptation of the jaw-mechanisms of these fishes is perfectly evident, a structural emphasis fitting them to an environment with poor supplies of food. In such surroundings it is an advantage to be able to take the largest possible meal that comes along, and at the same time, not to turn aside from a copepod. As Thorson, quoted by Moore (1958) has pointed out, the swallowing capacity of a predator must not only be proportional to the sparseness of the prey, but also be inversely related to its own speed of movement. (Moreover the copepod (or euphausiid) may at least be partly a carnivore and thus be well down the food-chain that begins with the plants of the surface-waters. Bogorov (1958) mentions that deep-sea copepods, such as *Pareuchaeta*, and *Bathycalanus* feed on radiolarians and other small animals. Some deep-sea decapods and amphipods are also carnivores.)

Despite their reduced economy of life, or rather because of it, these fishes are not to be regarded as 'misfits'. *Cyclothone microdon* is perhaps the most ubiquitous fish in the ocean, its range extending from subarctic to antarctic regions, although, the catches of mid-water nets are likely to give a 'false' impression of its abundance owing to its reduced activity. Off Bermuda, Beebe (1937) took eight times as many *Cyclothone* as lantern fishes, but the ocean must support greater numbers, certainly a greater weight, of the latter. (*Cyclothone* spp. are less easily recognized from a bathyscaphe than lantern fishes; thus experienced observers usually see more of the latter.)

Besides the regression of the muscular and skeletal systems, we have seen that the eyes and light-organs of these deeper living fishes are small in comparison with those of the species living above them. I have also implied that this economy of tissue must be linked to reduced development of the nervous and excretory tissues, a correlation which will also apply to the circulatory system. (A study of the alimentary system would also be of interest, for Nusbaum-Hilarowicz (1920) found the intestine of *Cyclothone* to be particularly simple in structure.)

Considering for the moment the eyes, if submarine sunlight is the only controlling factor in their development, the benthic fishes of the abyssal plain would be expected to have markedly regressed visual organs, but this expectation is by no means realized. As Hjort (Murray and Hjort, 1912) wrote: 'But if it be the case that the size of the eyes in pelagic fishes decreases vertically with the decreasing intensity of light, how can we explain the fact that the bottom fishes, like *Macrurus* (= *Nematonurus*) *armatus*, living in abyssal depths possess large and apparently well-developed eyes.' Perhaps this should be called Hjort's Paradox. However, the eyes of the abyssal macrourids and brotulids do tend to be relatively smaller than those of their relatives living over the continental slopes (Marshall,

1954),¹ and in a few species such as *Aphyonus gelatinosus*, the eyes are much reduced. These apparent exceptions will be discussed at a later point (pp. 111-112).

If we compare a black *Cyclothone*, an angler fish or a gulper eel with an abyssal bathypteroid, macrourid or a brotulid, the difference in the relative development of the eyes is not the only contrasting feature. Actually the bathypteroids have small eyes, but their myotomes and skeleton are far better developed, being almost as firm and well-knit as those of their shallow-water relatives, the lizard fishes (Synodontidae). A 3-ft. *Nematonurus armatus* is far better equipped with all manner of tissues than a 3-ft. gulper-eel (and it has kept its swimbladder). The small brotulid *Mixonus caudalis* is similarly 'better off' than a black *Cyclothone* or an angler fish. Many other such contrasts could be made, but here we need only add that the gill-surface of the benthic fishes is far better developed than that in the bathypelagic species.

But the deep-sea floor supports a larger standing crop of animal-life than do the deeper mid-waters of the ocean. In the Kurile-Kamchatka Trench region, which lies under a productive stretch of surface-water, the biomass of bottom-dwelling animals in a square metre was measured at 6.94 g., between depths of 950 and 4070 m. Between 5070 and 7230 m. the quantity fell to 1.22 g./m.³ (Zenkevitch and Birstein, 1956). Bottom samples taken by a Petersen grab from the 'Galathea' indicate that the deep-sea floor supports an average of ten animals per square metre with a total weight of about 1 g., and this must be a minimum value. Having given these figures, Spärck (1956) concludes thus: 'This surprising density right down to between 5000 and 8000 m. suggests that food conditions in the abyss are not so poor as we have been inclined to think, and this in turn leads us to suppose that abyssal water currents must be stronger than formerly believed.'

The key-organisms in the sediments, perhaps those at the base of the food pyramid, are the bacteria (Zobell, 1954; Zobell and Morita, 1956). They can exist on the dissolved organic matter in seawater and convert intractable substances such as cellulose and chitin into their own substance. The authors just mentioned suggest that the bacteria may be used directly as food, or may aid digestion by living as symbionts in the gut of bottom-dwelling animals. Whatever may be the actual conditions, it is clear that large standing-crops of mud-eating holothurians can exist at depths exceeding 6000 m. (Hansen, 1956). While these animals may be largely free from the attacks of predators, holothurians may still form 30-50 per cent of the biomass of benthic organisms in depths from 3000 to 7000 m., in regions where predatory groups such as the asteroids are particularly abundant (see Zenkevitch, 1954, fig. 2). Finally, at depths down to at least 2500 m., conditions of life at the bottom are favourable enough to attract detachments of active pelagic organisms, such as euphausiids, sergestids and lantern fishes (pp. 87-88).

It would thus seem that there is sufficient food on or near the bottom to satisfy the day-to-day requirements of the relatively highly organized bodies of bathypteroid, macrourid and brotulid fishes. As we have seen, species belonging to the second and third groups have retained a gas-filled swimbladder. There is structural and biological evidence that this organ is functional, even at great depths, but because of its decreased buoyant properties at high pressures some reduction of tissue density is necessary if the animals are to be in hydrostatic equilibrium with their environment. Furthermore, there is evidence that the muscular and skeletal tissues have been somewhat reduced. Even so, the level of development of these and other tissues is much superior to that possessed by the bathypelagic fishes poised above them in the deep, nutrient-poor waters of the ocean. In the endless struggle

¹ Moreover, *Nematonurus armatus* has a wide depth range (280-4600 m.) extending from regions receiving sunlight to unlit depths. In *Lionurus filicauda*, which seems to be restricted to the abyssal plain (2515-4846 m.), the eyes are proportionately smaller. A 500 mm. *Nematonurus armatus* has orbits measuring 18 mm. in diameter (Nybelin, 1957) while in a 400-mm. *Lionurus filicauda* the eyes are about 10 mm. in diameter.

for a living-space, interaction between fish and environment has been such that tissues have evolved not only to match the biological environment, but to conform to the physical stresses besides.

We are now in a better position to consider the deeper dwelling bathypelagic fishes. Presumably the species of *Cyclothone* once had a gas-filled swimbladder in the adult phase, but this is now only functional during larval life. *Gonostoma bathyphilum* has lost all trace of this organ, but it is well developed in a related species, *G. denudatum*. The ancestors of the ceratioid angler fishes and the gulper eels may also have had a swimbladder.

Now it is clear that the loss of this organ is not related to the pressure factor, or indeed, to any physical effect. The foregoing discussion simply suggests that the cause largely resides in the trophic conditions obtaining in the deeper mid-waters of the ocean. To begin with, a pelagic fish with a swimbladder is able to carry more muscle, attached to a firmer skeleton, than a fish (of comparable dimensions) without such buoyant uplift (Denton and Marshall, 1958). In turn, the proper maintenance and functioning of these tissues require well-developed circulatory, respiratory, alimentary, excretory and nervous systems. But with the loss of the swimbladder, the degree of tissue organization could become 'geared-down' to the low level of potential energy in the biological environment.¹ At the same time neutral buoyancy could be approached or, more likely, achieved.

Moving into the upper thousand metres of the ocean, it is surely significant that most of the plankton feeders, the small gonostomatids, hatchet fishes and lantern fishes possess a swimbladder (Marshall, 1951). Having this internal float, they are able to carry the muscle necessary to propel them upwards during their daily migrations to the food-rich surface-waters. It is also striking that most of the predatory fishes (Stomiidae, Melanostomiidae, Chauliodontidae, Idiacanthidae, Malacosteidae and Alepisauridae) lack a swimbladder. (The exceptions are *Astronesthes* spp. and *Chiasmodon niger*.) We have seen that (pp. 85-86) some of these fishes also undertake vertical migrations. It is probable that they, like *Gonostoma elongatum*, come close to neutral buoyancy through a reduction of skeletal and muscular tissue (Marshall, 1954, 1955; Denton and Marshall, 1958), but the regression of these tissues is by no means so marked as that in the pelagic fishes living in the deep, underlying waters.

Chauliodus sloanei is one of these predators living in the upper mid-waters. The younger individuals live fairly close to the surface and are thus well placed for food (Ege, 1948; Haffner, 1952). The deeper dwelling, older fishes grow to lengths of more than 250 mm.

During the daytime Dr Pérès has watched *Chauliodus* from a bathyscaphe and in a letter dated 17 November 1958 has written of his observations. These fishes hover in the water with the long axis of the body at an acute angle to the horizontal plane, the head being above the tail. At the same time the long second dorsal ray, which is tipped with luminescent tissue (Brauer, 1908), is curved forward over the head so that the extremity of the ray lies in front of the mouth. Clearly, the fish is behaving very much like a female ceratioid and is angling for prey. It is also looking obliquely upward, poised in a good position for detecting prey silhouetted against the down-going and scattered rays of sunlight, but towards sunset, it moves upwards to richer feeding grounds. While the density of its bone and muscle is less than that of a myctophid, it is much the larger fish, and what it lacks in unit muscle-power it gains in size and power of movement, which is also true of most of the other predatory fishes without a swimbladder. Moreover, it is interesting that the only predatory stomioids containing this organ are the species of *Astronesthes*, which are smaller than their predatory relatives without it (p. 90). Like its myctophid prey, *Astronesthes niger*, which crosses the upper thermocline during its migrations, has a firm skeleton and compact well-formed myotomes.

¹ If a teleost had both 'light weight' tissues and a capacious hydrostatic organ it would be overbuoyant.

But Hjort's Paradox is still unresolved. I have mentioned that certain of the brotulids are exceptional in having very regressed eyes. *Aphyonus gelatinosus* is such a species and it lacks a swimbladder. The tissues of its body are also much reduced by comparison with another brotulid of about the same size, *Mixonus laticeps*, a species with a swimbladder. This brotulid has an elongated tapering body, sheathed with scales and equipped with well-knit myotomes. The skeleton is quite firm. The eyes are small, but well-formed, with a wide pupil and a large lens. In the type specimen, which measures 125 mm. in standard length, the horizontal width of the eye-ball is about 4.0 mm.

As indicated by its specific name, *Aphyonus* has a gelatinous appearance. It is semi-transparent and colourless, except for deep-set points of pigment that represent the remains of the eyes. The skin is loose and scaleless, while the skeleton and myotomes are much reduced, the notochord being persistent.

While the type-specimen of *Aphyonus gelatinosus* is bulkier and somewhat longer (standard length 130 mm.) than that of *Mixonus laticeps*, it has a much simpler gill-system. On the first arch there are about fifty filaments with an average length of about 1.5 mm., the second arch bears about forty filaments, while there are only two to three on the fourth arch. *Mixonus laticeps* has somewhat shorter filaments but there are at least a hundred on the first arch and about eighty on the second. Moreover the filaments carry about twenty-five lamellae per millimetre, about twice as many as those developed in *Aphyonus*.

These contrasts are very like those already shown to exist between pelagic fishes from the upper and lower oceanic reaches. Perhaps *Aphyonus* is one of the deeper-living pelagic fishes. This genus, together with *Barathronus*, *Sciadonus* and *Leucochlamys* are placed by Nybelin (1957) in a new subfamily Aphyoninae, '... as they show many mutual similarities and in many respects differ from other Brotulids. As common characteristics may be mentioned a comparatively small body size, a thin loose scaleless skin without or with only very feeble pigmentation, strongly reduced eyes and bone tissues, and a more or less persistent notochord; an opercular spine, characteristic of the typical Brotulids, is lacking.' Moreover, they have very reduced gills and from Nybelin's figures of *Barathronus erikssoni* and *Sciadonus kullenbergi*, it is clear that a swimbladder is absent. As the cleft of the mouth runs obliquely upward in *Barathronus*, Nybelin has suggested that this genus is pelagic in habit. The only direct evidence is the rather young specimen of *Barathronus parfaiti* that was found by Legendre (1934) in the stomach of a long-finned tunny (*Thunnus alalunga*).

I suggest that the entire subfamily consists of deep-dwelling, bathypelagic fishes. If this proves to be so, the common characters might not be indicative of genetic affinity, but rather of convergent adaptation to their food-poor environment. (*Barathronus* and *Sciadonus* are viviparous, while the ovaries of the type of *Aphyonus gelatinosus* contain many eggs, suggesting oviparity.) The deeper mid-waters could even be regarded as a refuge for species that have been edged-out of the two main feeding grounds of the ocean, the waters under the interface between sea and atmosphere and those near the interface between sea and sediments.

If the Aphyoninae are not benthic fishes, the abyssal fauna consists almost entirely of species with small to moderately large eyes.¹ Now Denton and Warren (1957) suggest there are two main factors related to the size and development of the eyes in deep-water fishes. A fish living in the twilight zone is exposed to a large field of light, and here the size of the eye matters less than the relative proportion of the dioptric parts, a wide pupil being necessary. To perceive spots of luminescence efficiently a large collecting pupil is required; the bigger the eye the better. These conditions are met in fishes

¹ *Typhlonus nasus* is a blind brotulid and might be an exception, but it has a small, thin-walled swimbladder. The bones are soft and flimsy and the myotomes excessively thin. The eyes of *Ipnops* are not regressed but curiously modified. *Leucicoriscus*, which looks more like a bottom-dwelling brotulid, seems to be an exception (see also Marshall, 1954).

from the upper 1000 m., but what of the abyssal species? Their small to moderately large eyes are equipped with wide pupils and large lenses, and they have presumably retained their visual powers because there is luminescent light to be seen (some deep-sea bacteria are luminescent). Furthermore, at least some of them start life in the upper, lighted layers of the sea. (The same is true of the deep-dwelling pelagic species.) A flash of light may mean a euphausiid meal for a *Cyclothone*, or signify a predator. While the eyes of some of these fishes do not properly fulfil the second requirement, they have gone some way to meet it. However, the loss of the eyes in some pelagic fishes, that exist below the 1000-m. level, is compensated for by a marked development of the lateral-line organs on the head. *Aphyonus* has large canals and so has *Ditropichthys storeri*, which may well belong to this fauna (see also Marshall, 1954).

These considerations may seem far removed from swimbladder problems. But they have been set down because I once thought that the regression of the eyes and swimbladder might be linked to the disappearance of the pseudobranch. Myctophids, which have well-developed eyes and swimbladders also have large pseudobranchs. In *Gonostoma bathyphilum* and *Aphyonus gelatinosus*, with small or regressed eyes and no swimbladders, the pseudobranchiae are absent. Now Copeland (1952) found that removal of these organs in *Fundulus* inhibited the inflation of the swimbladder. Furthermore, the blood to the choroidal gland of the eye passes through the pseudobranch in teleosts, although the functional relationship is not clear (Barnett, 1951). However, despite a thorough search under the skin of the gill-chambers of *Astronesthes niger* and *Gonostoma denudatum*, fishes with swimbladders and large eyes, I was unable to find any trace of pseudobranchiae.

We have seen that the loss of the swimbladder in pelagic fishes of the deeper, mid-oceanic waters is not related to the pressure factor, but rather to their harsh biological environment, one that seems to be lacking in the potential energy required to maintain the extra tissues associated with an internal float. Is the regression of the eyes in such fishes as the Aphyoninae, the Monognathidae and *Cyclothone obscura* also to be explained on this basis? Is this a further economy of living tissue?

In dealing with blind cave fishes, Walls (1942) points out that the elimination of the eyes is but a small economy, most of the energy released from food going into motor and secretory activity. However, there is an associated saving of tissue in the central nervous system in the form of a much reduced optic tectum (see Marshall and Thines, 1958). On the other hand, Heuts (1951) maintains that the slow growth-rates, low metabolism and regressed tissues (including the eyes) in *Caecobarbus* are adaptations to the limited food resources of the environment. He goes on to suggest that this is true of all cave fishes. But this is too sweeping a generalization, as Breder (1953) and Cahn (1958) have shown. Some cave fishes, such as *Anoptichthys jordani*, may have good supplies of food and they are most active animals. An *Anoptichthys*, which has a well-developed swimbladder, carries much more muscle than a *Cyclothone microdon* of the same size. Apart from these considerations, caves differ from the deep mid-waters of the ocean in being totally dark.

To return to blind deep-sea fishes, Heuts's concept of the regression of the visual tissues seems more applicable to their case than to the condition found in some cave fishes. While economy in the form of reduced visual and nervous tissue is a small item in the energy balance sheet of an *Anoptichthys*, it might well be critical for an *Aphyonus*. As if to compensate for its loss of vision, *Aphyonus* has a well-developed 'Ferntastsinn' sense in the form of neuromast organs on the head. Do these require less energy to maintain than eyes? At all events, they require smaller centres in the brain. Here the problem may be left with the thought that the food-factor may well be critical, but it may not be the only factor involved.

We are left with certain concepts, which are partly summarized in Text-fig. 47. Living in the ocean at depths above 1000 m. are several hundred species of pelagic plankton-feeding fishes with

well-formed, gas-filled swimbladders. They are muscular, active little fishes with large eyes and brains and highly developed light-organs. Because of the extra propulsive power that a swimbladder allows, they are able to make daily visits to the food-rich, surface-waters, which they must do to maintain their highly organized bodies. Living with them are almost as many predatory fishes, nearly all of which have lost an internal float. In spite of this, these fishes come close to neutral buoyancy by reducing their muscular and skeletal tissues. All have well-formed eyes and brain, and many have complex batteries of light organs. Some of these fishes also migrate to the surface-layers, compensating for their reduced myotomes by increased size of body.

Living below them in the deep mid-waters, are more than a hundred species of pelagic fishes with no swimbladders and very reduced tissues. They are nearly all predatory fishes, many of which lure their prey instead of pursuing it. As they are likely to be neutrally buoyant they can hover in the water without undue effort. The energy balance sheet of these species seems closely fitted to the limited supplies of potential energy around them.

On the abyssal plain, about 250 species of benthic fishes have been taken below a depth of 2000 m. Well over half have well-formed swimbladders and a number of species may range as deeply as 5000 m. Compared with the deeper bathypelagic fishes they are highly organized, but show some reduction of bone and muscle to compensate for the reduced positive buoyancy of a swimbladder at great depths. Most of the species without a swimbladder have an equally good organization, but the food supply seems sufficient to satisfy their day to day requirements.

These differences in form and organization of the tissues are reminiscent of Raunkiaer's (1934) concept of life form in plants.¹ 'All over the world environments varying from place to place determine the existence of different life forms, because the demands of the plants, which are, at any rate, partially expressed by their structure, must of necessity be in harmony with the environment if life is to continue.' Raunkiaer saw that certain structural features were correlated with certain types of environment and that these features were shared by diverse species of plants. Reference to this section, particularly to the table on p. 105, will show that this is also true of the assemblages of fishes that live at the upper and lower levels of the bathypelagic environment. As I hope to continue with this problem, to look more closely at some of the knots in Bigelow's (1930) 'endless web of netting', these few remarks will suffice to conclude this Report.

SUMMARY

STRUCTURAL DEVELOPMENT OF THE SWIMBLADDER (pp. 6-50)

Dissection of about ninety species of bathypelagic teleosts has shown that a well-developed, gas-filled swimbladder is present in numerous stomiatoid fishes (most Gonostomatidae, Sternoptychidae, *Astronesthes* spp.); salmonoid fishes (*Opisthoproctus*, *Winteria*) Myctophidae (most species), Melamphaidae (most species) and *Chiasmodon niger* (Chiasmodontidae). The swimbladder regresses during adult life in the Miripinnati, certain of the Stomiidae and a few Myctophidae and Melamphaidae. It is completely absent in numerous stomiatoids (Melanostomiidae, Chauliodontidae, Idiacanthidae and Malacosteidae), Alepocephalidae, certain Myctophidae, Scopelosauridae, Alepisauridae, Giganturoidea, Lyomeri and Ceratioidea.

¹ Certain continental zoologists have also developed the idea of 'Lebensformtypen' in animals (see Macfadyen, 1957), but the concept is more familiar to botanists.

SWIMBLADDER STRUCTURE AND CLASSIFICATION (pp. 50-58)

The structural plan of the swimbladder has thrown new light on the classification of these groups. The stomiatoids are revealed as a compact (paraphysoclistous)¹ group with a single, bipolar rete mirabile at the posterior end of the swimbladder which has a resorbent capillary bed, obtaining its arterial blood through a by-pass branch of the retial artery. Differences in swimbladder structure may also be useful in distinguishing genera.

The deep-sea salmonoid fishes have a very different (euphysoclistous)¹ form of swimbladder with micro-retia mirabilia supplying the gas-gland. The myctophid swimbladder is also euphysoclistous (with an oval) and three unipolar retia mirabilia enter the anterior end of the sac to carry blood to the three-lobed gas-gland. The families Anoplogastridae, Melamphaidae and Stephanoberycidae (sub-order Anoplogastroidea, Berycomorphi) yet again have a euphysoclistous swimbladder (with an oval) and one or two unipolar retia mirabilia, which run forward from the posterior end of the sac. These and other findings are used to discuss the development of a closed swimbladder in the deep sea, particularly in the predominantly physostomatous¹ Isospondyli, and to consider evolutionary relationships.

THE SWIMBLADDER WALL (pp. 59-65)

The fine structure of the swimbladder wall in bathypelagic teleosts is much like that of other physoclistous groups. Excluding the peritoneal investment, an outer, thin but tough layer of collagen fibres (tunica externa) is separated from the inner epithelial layer by a more voluminous reticulum of fibres developed within a semi-fluid, gelatinous matrix. There is also a layer of smooth muscle fibres near the inner epithelium. Following descriptions of the fine structure of the swimbladder wall in certain species, there is some discussion of its mechanical and gas-proofing qualities. In particular, attention is drawn to the rôle of the submucosa in a swimbladder undergoing compression during a migration into deeper waters. The semi-fluid submucosa would seem to allow the tissues to relax in a uniform manner and the sac to maintain its ellipsoidal shape.

FAT-INVESTED SWIMBLADDERS (pp. 65-68)

In certain bathypelagic fishes (the stomiatoids, *Cyclothone* spp., *Gonostoma elongatum*, *Polyipnus laternatus*, *Borostomias antarcticus*, *Stomias colubrinus*, *S. affinis*, the myctophids, *Lampanyctus leucopsarus*, *Diaphus theta* and the anoplogastroid, *Anoplogaster longidens*), the swimbladder regresses after metamorphosis and becomes invested with fat, which is deposited between the peritoneum and the tunica externa. It is pointed out that this replacement of gas by fat can have but little effect on the 'credit side' of the 'buoyancy balance sheet'.

THE SWIMBLADDER AS A HYDROSTATIC ORGAN AND THE STRUCTURE OF THE GAS-PRODUCING AND RESORBENT PARTS (pp. 68-81)

Like species living nearer the surface or over the continental slope, the volume of the swimbladder in bathypelagic fishes is about 5 per cent of the body volume. It thus functions as a hydrostatic organ, making its possessor weightless in water. But compared to shallow-water species the gas-producing complex (rete mirabile and gas-gland) is highly developed:

1. The product of the number and length of the capillaries forming the retia is high compared to the dimensions of the swimbladder. These two features, together with the form of arrangement of the capillaries, are also considered in relation to the design of the retia as counter-current systems allowing

¹ See p. 50.

of gaseous exchange between the arterial and venous capillaries. There is evidence that the deeper living species tend to have longer retia.

2. The development of the gas-gland, as expressed by its surface area, is much more pronounced in bathypelagic than in epipelagic species. There appear to be three main types of gas-glands; (a) with many giant cells, (b) with medium sized cells, and (c) with small cells. Intracellular capillaries are found in the first type. Certain cytological features of the gas-gland cells of *Vinciguerrria* seem in keeping with the accumulating evidence that the cells actively transport gases from the blood plasma to the lumen of the swimbladder.

The structural features of the resorbent part of the swimbladder, the part by means of which the gas-content can be reduced, are reviewed. Certain aspects of form and function are considered.

THE SWIMBLADDER AND VERTICAL DISTRIBUTION (pp. 82-85)

A well-developed gas-filled swimbladder is only to be found in *bathypelagic* fishes with centres of concentration *above* the 1000-m. level. While numerous other species in the same environment lack such a swimbladder, this condition is universal in bathypelagic species that occur *below* a depth of 1000 m. The loss of the swimbladder in the deeper living species might seem to be related to the pressure factor, to the compressibility of gases and the amounts of energy and gas required to keep the swimbladder inflated at the appropriate buoyant volume against high hydrostatic pressures.

THE SWIMBLADDER AND VERTICAL MIGRATIONS (pp. 85-95)

Many of the *bathypelagic* fishes living in the upper oceanic reaches (200 to 1000 m.) undertake diurnal vertical migrations. After reviewing the evidence for these movements, the physical and biological background of these migrations is considered. While a number of species cross the near-surface thermocline during their upward migrations, other species are rarely if ever taken in the surface-layers and may be called partial migrators. The physical problems of gas secretion and resorption are considered for both types of migrator. While these fishes are small, active species with a relatively large gill-surface, the provision of enough gas to fill the swimbladder during and after a downward migration seems an immense physiological task unless the gas-gland can store oxygen in a combined form. Concerning the loss of gas during an upward migration, the high ratio between the resorbent surface and the volume of the swimbladder and the very steep concentration gradient between the tensions of the swimbladder gases and those in the blood, may well mean that the rate of gas resorption is high enough to keep pace with the reduction in hydrostatic pressure.

THE SWIMBLADDER AND THE ECONOMY OF LIFE IN THE DEEP SEA (pp. 95-113)

At least half of the *benthic* species that range below a depth of 2000 m. have well-developed, gas-filled swimbladders, with very long retia mirabilia. Considering also the *bathypelagic* species, there is a direct correlation between the length of the retia and the depth of the living space, a further striking indication of the function of the retia as systems for the counter-current exchange of gases. Apart from implying that the swimbladders of these fishes are functional at great depths (down to 5000 m.) these facts suggest that the loss of the swimbladder in bathypelagic fishes with centres of concentration below the 1000-m. level is not due to the pressure factor. The most potent influence is seen to be the food-poor environment of these fishes, one without the necessary nutriment to support the 'extra' tissues that can be carried at neutral buoyancy by a hydrostatic organ. Compared with the fishes with swimbladders living in the upper reaches (200-1000 m.) of the bathypelagic environment (and with benthic species), the tissues of these deeper living species are much regressed. The life-forms of diverse fishes from these different levels are no less striking than those found in plants.

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PLATE I

Microphotographs of transverse sections through the swimbladder.

- Fig. 1. *Vinciguerria nimbaria*; section cut towards the posterior end of the swimbladder between the rete and gas-gland ($\times 150$). Note the artery-vein pairs (each an association of a large and small vessel) running to the gas-gland and the undulating appearance of the fibres in the submucosa.
- Fig. 2. Section through the regressed swimbladder of *Cyclothone livida* ($\times 300$). Note the capillaries of the regressed rete mirabile and the regressed cells of the gas-gland (mainly to be seen in the upper right half of the section. See also text fig. 34).
- Fig. 3. Section through the rete of *Polyipnus laternatus* ($\times 130$). Note the section cut through the by-pass branch of the retial artery at the top of the photograph.
- Fig. 4. Enlarged part of Fig. 3 ($\times 580$). The 'triangle' of nuclei (at about 7 o'clock) in Fig. 3 will be again seen in this figure. The larger capillaries in this section belong to the venous part of the retial circulation.

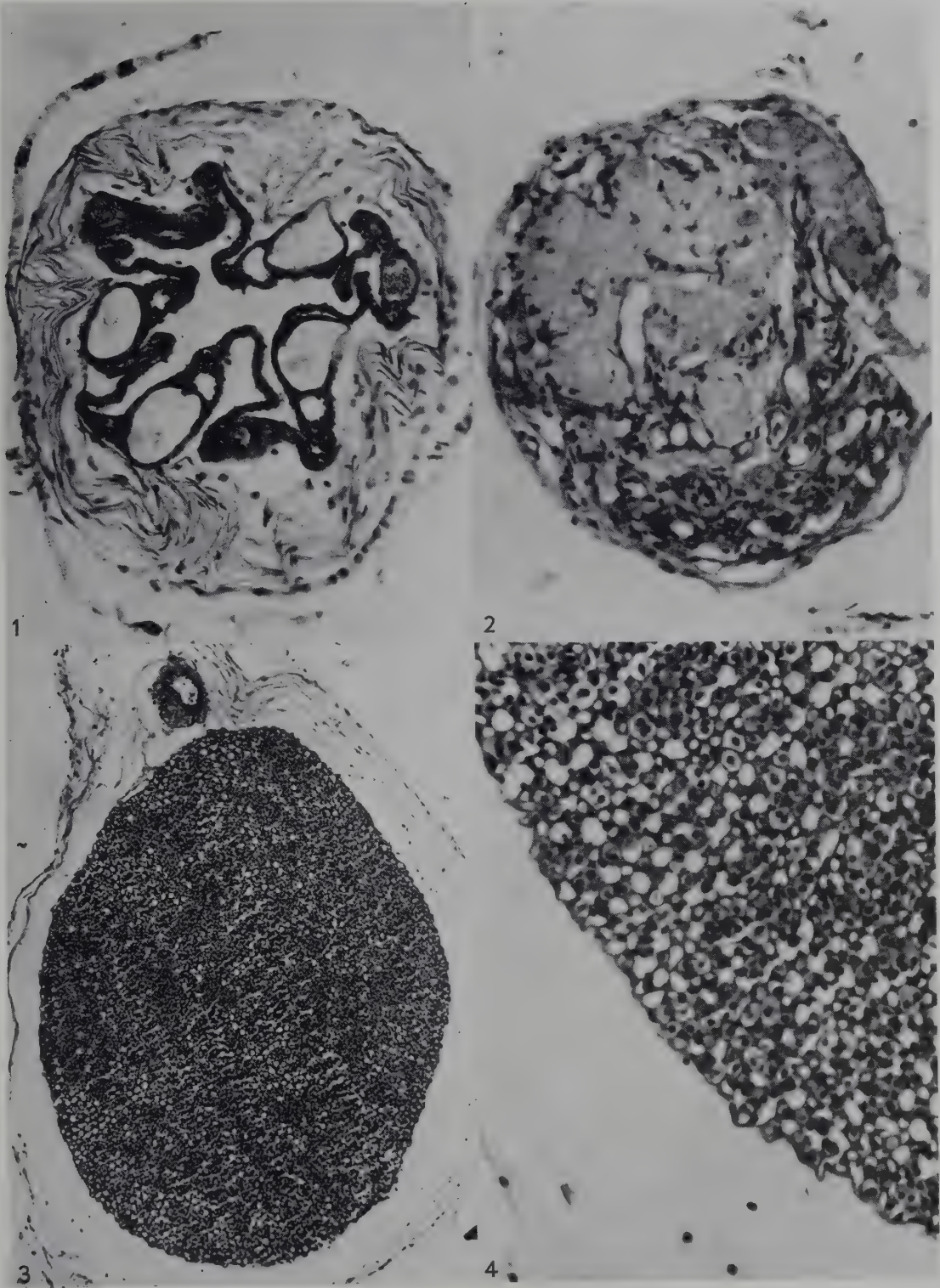


PLATE II

Microphotographs of parts of the swimbladder, taken from sections (figs. 1-3, transverse section; fig. 4 longitudinal section).

- Fig. 1. Giant cell of gas-gland of *Vinciguerria attenuata* ($\times 675$). Note the intracellular capillaries, surrounded by lighter staining pericapillary cytoplasm and the fine canals joining the capillaries. The vacuolated nature of the pericapillary cytoplasm can also be seen. *b* = base of cell.
- Fig. 2. Much enlarged part ($\times 1500$) of a giant gas-gland cell of *Vinciguerria attenuata* to show the vacuolated nature of the cytoplasm surrounding the capillaries.
- Fig. 3. Appearance of part of the gas-gland in a compressed swimbladder of *Vinciguerria nimbaria* ($\times 225$). Note the very different shape of the cells from the one shown in fig. 1, which came from a fully expanded swimbladder. The intracellular capillaries and pericapillary cytoplasm (here without vacuoles) may also be seen.
- Fig. 4. Entry of a rete into lobe of gas-gland of *Myctophum punctatum* ($\times 67.5$). Note the parallel system of capillaries forming the rete and the capillaries running among the gas-gland cells.

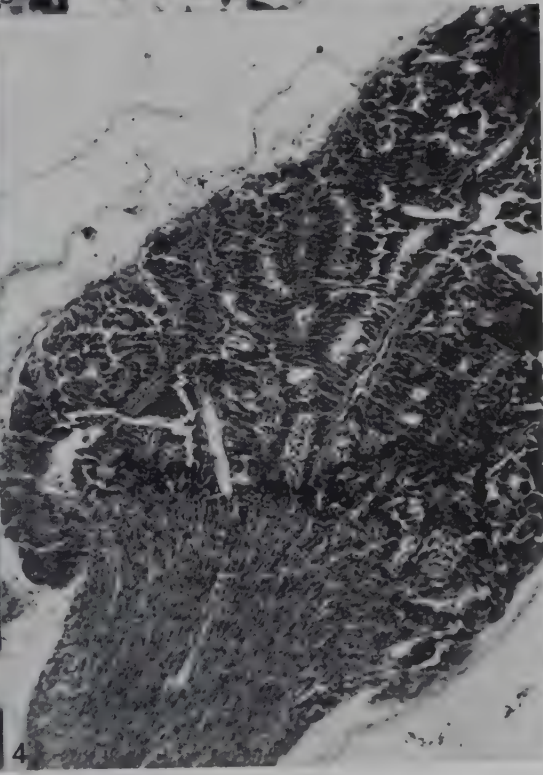
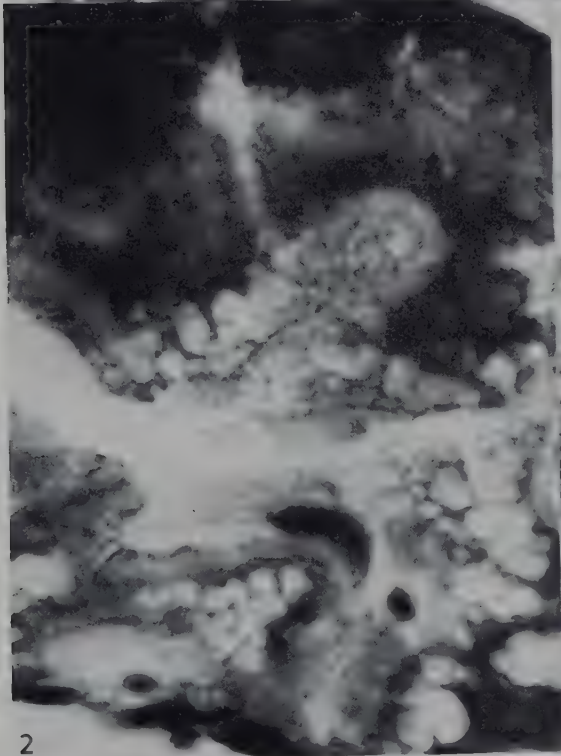
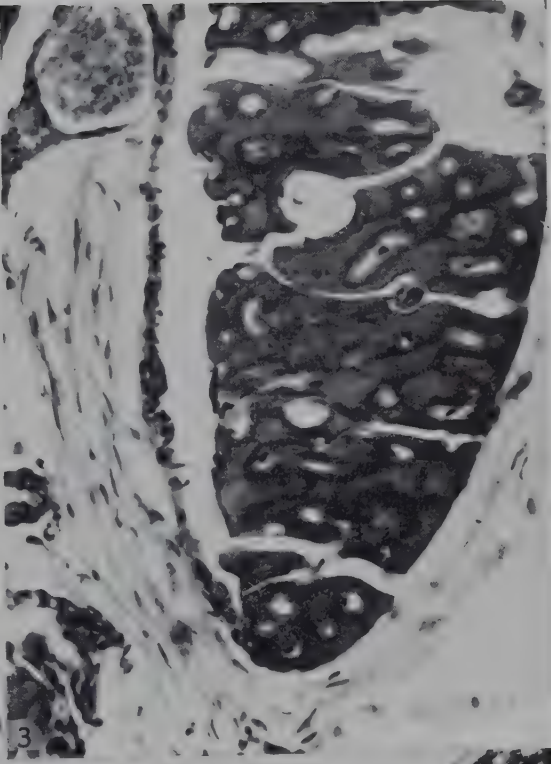


PLATE III

Fig. 1. Microphotograph of longitudinal section of a much contracted oval in the swimbladder of *Myctophum punctatum* ($\times 120$). Note the many blood vessels running through the relaxed tissues of the oval, mostly consisting of the submucosa. The radial muscles of the oval (*rm*) may be clearly seen. An arrow in the main cavity of the swimbladder points to the almost completely closed opening of the oval.

Fig. 2. Radiographs of *Trisopterus minutus* (above) and *Lionurus filicauda* ($\times 1$). Note the very much sharper appearance of the bones of the former.



1



2

